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UTILISATION DE L'HABITAT, CROISSANCE, CONDITION, SURVIE APPARENTE, ET DÉPLACEMENTS DE L'OMBLE DE FONTAINE (*SALVELINUS FONTINALIS*) ET DU SAUMON ATLANTIQUE (*SALMO SALAR*) EN SYMPATRIE

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RÉSUMÉ

La coexistence de l'Omble de fontaine et du Saumon atlantique juvénile dans les milieux lotiques est favorisée par la ségrégation spatiale des deux espèces entre les fosses et les rapides. Les fosses et les rapides sont des habitats très distincts. Entre autres, les densités d'invertébrés dans la dérive et sur le substrat, et la vitesse du courant sont supérieures dans les rapides. Ainsi, les coûts (maintien de la position, déplacements) et bénéfices (nourriture) associés à l'utilisation de l'un ou l'autre de ces habitats sont manifestement différents. Puisque la sélection de l'habitat chez l'Omble de fontaine et le jeune Saumon atlantique en ruisseau semble influencée par des comportements à caractère agressif (territorialité et dominance), et que les individus dominants occupent généralement les meilleurs habitats, les modèles de sélection de l'habitat prédisent que, pour chaque espèce, la profitabilité moyenne devrait être plus grande dans le meilleur habitat. Pour vérifier cette hypothèse, nous avons comparé trois mesures de profitabilité soit la croissance, la condition, et la survie apparente de chaque espèce entre les fosses et les rapides. Nous avons également étudié la distribution spatiale de l'omble et du saumon entre les fosses et les rapides. Puis, nous avons quantifié les déplacements afin 1) d'évaluer la fidélité à un site ou à un habitat particulier, 2) de voir si les déplacements entre les habitats sont directionnels et 3) d'estimer l'influence des densités de compétiteurs (hétérospécifiques et conspécifiques) sur les déplacements.

Les ombles et les saumons ont été suivis durant les étés de 1993 et 1994, dans deux ruisseaux de l'est du Québec, en utilisant des techniques de marquage-recapture. Les poissons étaient récoltés par pêche électrique dans neuf paires de sections, chaque paire

étant composée d'une fosse adjacente à un rapide. Les sections étaient échantillonnées à trois reprises durant l'été, soit à la mi-juin (marquage), à la mi-juillet (marquage-recapture), et à la mi-août (conservation des recaptures). Chaque individu était mesuré (longueur à la fourche), pesé, et marqué. Les ombles et saumons ≥ 55 mm étaient tatoués avec du bleu d'alcian sur les nageoires pectorales, pelviennes, ou caudale, en utilisant un code spécifique au lieu et à la date de capture. Chaque individu ≥ 55 mm recevait aussi une micro-étiquette à numérotation binaire (« *coded wire tag* », CWT) l'identifiant de façon individuelle. Quant aux poissons < 55 mm, ils étaient marqués en coupant leur nageoire adipeuse et une de leur nageoire pelvienne de façon à les identifier à l'habitat de marquage.

Toutes les marques de bleu d'alcian sont demeurées clairement visibles pour une période d'environ quatre semaines (entre 24-29 j). Après environ huit semaines (entre 52-65 j), 2,2 % des 91 ombles et 6,2 % des 64 saumons recapturés avaient perdu au moins une marque. La rétention du bleu d'alcian était faible chez les individus recapturés 10-14 mois après l'injection, probablement parce que la croissance de ces individus a provoqué la dilution des pigments de teinture. Les taux de pertes de CWT étaient 4,5 % pour l'omble et 11,8 % pour le saumon quatre semaines après le marquage, et 1,1 % pour l'omble et 5,9 % pour le saumon après huit semaines. Les marques n'ont semblé avoir aucun effet négatif sur la croissance et la condition des recaptures, quatre et huit semaines après le marquage.

Durant l'été, les ombles d'âge ≥ 1+ étaient significativement plus abondants dans les fosses que dans les rapides alors que les ombles 0+ et les saumons occupaient les deux habitats plus équitablement. La fidélité au site était élevée puisque la majorité des recaptures

étaient retrouvées dans la paire fosse-rapide où elles avaient été marquées (omble = 95,4 %; saumon = 91,2 %; longueur moyenne des paires = 24,0 m). Le taux de mouvement de l'omble était significativement plus élevé des rapides vers les fosses alors que celui du saumon était significativement plus élevé des fosses vers les rapides. La taille et les densités de compétiteurs n'influençaient pas significativement la portée des déplacements. Les patrons d'occupation et de changement d'habitat supportent l'hypothèse selon laquelle, en sympatrie, le saumon, plus agressif que l'omble, déplace celui-ci des rapides vers les fosses.

La croissance et la condition des deux espèces étaient semblables dans les fosses et les rapides. La survie apparente du saumon était significativement meilleure dans les rapides. Bien qu'en moyenne supérieurs dans les fosses, les estimés de survie apparente pour l'omble étaient très variables et statistiquement semblables dans les deux habitats. Ces résultats suggèrent que la distribution du saumon est « non-libre » et probablement influencée par la dominance. Pour l'omble, nous n'avons pas pu rejeter l'hypothèse d'une distribution libre idéale.

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INTRODUCTION

L'écologie des populations de salmonidés a suscité beaucoup d'intérêt en recherche, particulièrement depuis la fin des années cinquante. Plusieurs représentants de cette famille, tels le Saumon atlantique (*Salmo salar*) et l'Omble de fontaine (*Salvelinus fontinalis*), font l'objet d'une pêche sportive ou commerciale très intensive. Par conséquent, beaucoup d'efforts ont été déployés pour améliorer notre compréhension de la dynamique de ces populations, afin de mieux les gérer. Par exemple, concurremment au développement de la pisciculture, l'étude de la compétition intraspécifique est apparue très importante. De plus, avec la multiplication des ensemencements, beaucoup d'efforts ont été déployés pour étudier les effets de la compétition intra- et inter-spécifique sur les populations introduites et résidentes. La coexistence de différentes espèces de salmonidés est souvent reliée à leur utilisation différentielle de l'habitat et une compréhension approfondie des mécanismes qui régissent celle-ci est essentielle pour estimer les effets que pourraient avoir une modification importante de la structure d'un cours d'eau sur des populations naturelles ou non.

Il arrive souvent que différentes espèces de salmonidés habitent les mêmes cours d'eau. En Amérique du nord, les exemples de populations sympatriques sont nombreux (revue dans Hearn 1987): l'Omble de fontaine et le Saumon atlantique, la truite brune (*Salmo trutta*) et le Saumon atlantique, l'Omble de fontaine et la truite arc-en-ciel (*Oncorhynchus mykiss*), la truite arc-en-ciel et le Saumon chinook (*Oncorhynchus tshawytscha*), l'Omble de fontaine et la truite fardée (*Salmo clarki*), le Saumon chinook et le Saumon coho (*Oncorhynchus kisutch*), etc. Cependant, plusieurs de ces associations ne sont

pas naturelles et résultent de l'introduction d'espèces exotiques par le biais d'ensemencements. Lorsque les exigences des espèces sympatriques en termes d'habitat et de nourriture sont très similaires, il y a une forte compétition et le moins bon compétiteur est désavantagé (Rose 1986; Glova et Field-Dodgson 1995). Ces sympatries non-naturelles se soldent parfois par l'exclusion de l'une des espèces (Larson et Moore 1985). Inversement, d'autres associations perdurent et apparaissent plutôt stables, comme celle de l'Omble de fontaine et du Saumon atlantique juvénile.

La coexistence d'espèces sympatriques peut être facilitée par des différences d'utilisation de l'habitat entre les espèces; c'est la ségrégation spatiale (Nilsson 1967; Jones 1975). La ségrégation spatiale est dite « interactive » lorsqu'elle résulte de la compétition entre les espèces, et « sélective » lorsque des différences innées et possiblement adaptatives influencent la distribution des espèces (Nilsson 1967). Ainsi, la ségrégation spatiale peut être favorisée par des différences spécifiques en regard de l'agressivité, la préférence innée d'habitat, la morphologie, et la période d'émergence, ou d'une combinaison de ces facteurs (Hearn 1987).

Dans l'est du Canada, le Saumon atlantique fraye communément dans les cours d'eau où habite l'Omble de fontaine. Donc, durant les deux à trois premières années en eau douce, le saumon juvénile vit en sympatrie avec l'omble. Généralement, durant l'été, l'omble est plus abondant dans les fosses, et le saumon, dans les rapides (Gibson 1973; Power 1980; Randall et Paim 1982). Gibson (1973) a observé qu'en sympatrie durant l'été, lorsque la

nourriture est abondante, l'omble et le saumon sont abondants dans les rapides. Cependant, lorsque la nourriture devient plus rare, le saumon demeure abondant dans les rapides, mais l'omble quitte les rapides et se concentre dans les fosses. Il semble que cette ségrégation spatiale de l'omble et du saumon, entre les fosses et les rapides, résulte à la fois d'une compétition par exploitation et d'une compétition par interférence (Gibson 1973).

Le saumon est morphologiquement mieux adapté que l'omble pour maintenir sa position dans les eaux rapides. En effet, il possède des nageoires pectorales très larges et une flottabilité faible, adaptations lui permettant de rester en contact avec le substrat et de se maintenir dans des courants très forts et ce, parfois même sans nager (Keenleyside 1962; Gibson 1981). L'omble doit par contre nager activement pour maintenir sa position dans le courant, ce qui exige des dépenses énergétiques importantes (Keenleyside 1962). Les caractéristiques morphologiques du saumon lui permettent d'exploiter les eaux vives plus efficacement que l'omble et, par conséquent, d'être un meilleur compétiteur dans les rapides (Gibson 1973).

La ségrégation spatiale semble également favorisée par des différences d'agressivité entre les espèces (Gibson 1973). Peu après leur émergence du gravier, les jeunes ombles et saumons deviennent rapidement territoriaux ou forment des hiérarchies de dominance (Keenleyside 1962; Griffith 1972; Symons et Heland 1978; McNicol et Noakes 1981, 1984). Ces deux espèces de salmonidés utilisent les mêmes comportements ou signaux pour communiquer lors de rencontres à caractère agressif (Gibson 1973, 1978, 1981). Des études

menées dans des bassins expérimentaux ont démontré que les jeunes saumons sont beaucoup plus agressifs que les jeunes ombles, puisqu'ils débutaient et remportaient la majorité des attaques interspécifiques (70 % des attaques interspécifiques étaient remportées par le saumon alors que l'omble était vainqueur dans seulement 30 % des cas; Gibson 1973). Ainsi, le saumon pourrait repousser l'omble hors des rapides lorsque la nourriture devient limitante (Gibson 1973; Gibson et Galbraith 1975). D'autre part, l'omble, dont l'émergence précède celle du saumon d'environ deux à trois semaines (Randall 1982), semble rivaliser plus efficacement avec le saumon dans les fosses, bénéficiant d'un avantage au niveau de la taille. Dans les fosses, l'omble pourrait se protéger de la compétition avec le saumon en formant des groupes de plusieurs individus (Keenleyside 1962; Gibson 1973). Donc, l'utilisation de l'habitat par l'omble et le saumon serait fortement influencée par les caractéristiques physiques de l'habitat (vitesse du courant, profondeur, substrat) et par la présence d'individus dominants ou agressifs.

Selon les modèles théoriques de sélection d'habitat en fonction de la densité, la sélection de l'habitat chez les individus habitant dans un environnement hétérogène sera influencée par le choix des autres individus rivalisant pour les mêmes ressources limitées. Chaque membre de la population se distribue dans l'environnement de façon à maximiser son fitness. Dans la théorie de la distribution libre idéale (Fretwell et Lucas 1970), la sélection de l'habitat n'est pas influencée par des comportements agressifs et les individus sont libres de se déplacer d'un habitat à l'autre. Le meilleur habitat est colonisé jusqu'au moment où il devient plus profitable aux nouveaux arrivants d'occuper un habitat de qualité

inférieure à cause de la diminution des ressources surexploitées dans le meilleur habitat. Le fitness moyen demeure égal entre les habitats jusqu'à ce que ceux-ci soient saturés. Cependant, l'utilisation des ressources peut être restreinte par l'activité d'individus dominants ou territoriaux qui monopolisent les ressources et en privent les autres individus. Selon les modèles de distribution idéale despotique (Fretwell et Lucas 1970) et idéale par préemption (Pulliam et Danielson 1991), les nouveaux venus sont forcés par les dominants à occuper des habitats de qualité inférieure. Ces modèles prédisent que le fitness moyen devrait être inférieur dans l'habitat le plus pauvre.

Puisque chez l'Omble de fontaine et le Saumon atlantique, la sélection de l'habitat est influencée par des interactions à caractère agressif, certains individus, les compétiteurs supérieurs, devraient occuper les endroits (ou habitats) qui leur sont plus favorables (Fausch 1984; Metcalfe 1986; Rincón et Lobón-Cerviá 1993). Les compétiteurs inférieurs, quant-à eux, devraient occuper les endroits (ou habitats) sous-optimaux. Peu d'informations quantitatives à ce jour permettent de vérifier cette hypothèse. Nous ne savons pas s'il existe des différences de profitabilité entre les fosses et les rapides chez l'omble et le saumon vivant en sympatrie. Cependant, l'omble et le saumon s'alimentent principalement de la dérive d'invertébrés (Keenleyside 1962; Gibson et al. 1984; Thonney et Gibson 1989). Or, il est reconnu que la quantité d'insectes dans la dérive augmente proportionnellement à la vitesse du courant (Chapman et Bjornn 1969; Everest et Chapman 1972; Wankowski et Thorpe 1979; Fausch 1984) et que les invertébrés aquatiques sont plus denses dans les eaux rapides (Schlosser et Ebel 1989). De ce point de vue, on pourrait s'attendre à ce que les rapides

soient l'habitat préférentiel des deux espèces. En effet, bien que l'omble soit moins bien adapté que le saumon pour maintenir leur position face à un courant violent, les salmonidés en ruisseau choisissent généralement les sites offrant le gain énergétique net potentiel le plus élevé (calcul basé sur l'énergie disponible dans la dérive moins le coût de la nage sur place; Fausch 1984). Ces sites sont ordinairement ceux présentant la plus grande différence de vélocité de l'eau (soit la différence entre la vélocité au point focal et la vélocité maximale dans un rayon d'environ 60 cm du poisson; Fausch et White 1981). L'omble et le saumon pourraient représenter un exemple du modèle polyspécifique de sélection d'habitat dit de préférences partagées (« shared preferences ») de Pimm et al. (1985). Selon ce modèle, lorsque deux espèces préfèrent le même habitat (rapides), l'espèce dominante (saumon) repousse l'espèce subordonnée (omble) vers l'habitat secondaire (fosses). Bien que la sélection de l'habitat de l'omble et du saumon en sympatrie soit bien connue, il n'existe aucune preuve que le succès de chaque espèce diffère entre les fosses et les rapides. Des informations pertinentes à ce sujet pourraient être acquises en comparant, pour chaque espèce, des indices de profitabilité (ou mesures indirectes du fitness) entre les fosses et les rapides.

L'étude des mouvements des deux espèces en regard des habitats s'avère également essentielle pour bien comprendre la dynamique des populations sympatriques d'omble et de saumon. Par exemple, il est important de savoir si les individus de chaque espèce demeurent fidèles à un site et un habitat particulier durant l'été, si les déplacements entre les habitats sont fréquents et s'ils sont directionnels, c'est-à-dire des rapides vers les fosses ou vice-

versa. Il est également important de savoir si la taille influence les déplacements. Si les individus subordonnés sont expulsés des meilleurs sites par les dominants, les petits individus devraient avoir des taux de mouvements plus importants que les grands (Riley et al. 1992). À ce jour, les informations quantitatives détaillées sur les déplacements des deux espèces en sympatrie sont rares. Durant la période estivale, les déplacements de l'omble et du jeune saumon sont restreints et la majorité des individus demeurent fidèles à une section spécifique dans le cours d'eau (Keenleyside 1962; Saunders et Gee 1964; Randall et Paim 1982). Saunders et Gee (1964) ont même observé que certains jeunes saumons, ayant été déportés à plus de 213 m de leur site de capture initiale, ont été recapturés dans celui-ci peu de temps après. Cependant, bien qu'à un moment donné les populations de salmonidés soient composées d'une large fraction d'individus stationnaires, il demeure une petite fraction d'individus mobiles (Funk 1955; Solomon et Templeton 1976). La caractérisation des individus mobiles apparaît importante afin de mieux comprendre les interactions intra- et interspécifiques. En effet, la compétition peut être une importante cause de mouvement (Chapman 1962). Les individus dominants occupent ordinairement les endroits ou les habitats les plus favorables, et ils repoussent les compétiteurs inférieurs vers les sites ou habitats sub-optimaux (Fausch 1984; Fausch et White 1981). Manifestement, les coûts et les bénéfices associés à chacune de ces stratégies (être stationnaire ou se déplacer) sont très différents (Puckett et Dill 1985; Elliott 1990). Les individus territoriaux, qui se déplacent généralement peu, ont un bilan énergétique supérieur à celui des autres individus. Ces poissons investissent moins d'énergie dans la recherche et la capture des proies, ainsi que dans les activités à caractère agressif (Puckett et Dill 1985). Elliott (1990) a aussi démontré

que la survie, durant les premiers stades de la vie des salmonidés, était étroitement liée à la possession d'un territoire.

Il est essentiel de bien comprendre les différences de profitabilité entre les habitats pour interpréter la dynamique des populations habitant un milieu hétérogène (Pulliam et Danielson 1991). Plusieurs études ont permis de mettre en évidence l'importance de l'habitat dans la distribution spatiale de l'Omble de fontaine et du Saumon atlantique en sympatrie. Cependant, les effets de l'habitat sur la profitabilité moyenne et les déplacements de chaque espèce demeurent inconnus.

Ce travail présente, en trois chapitres, les résultats d'une étude sur l'écologie des populations sympatriques naturelles d'Omble de fontaine et de Saumon atlantique juvénile. Durant deux été consécutifs, les ombles et les saumons de deux ruisseaux de l'est du Québec ont été suivis individuellement, en utilisant des techniques de marquage-recapture. Dans un premier temps (chapitre 1), nous avons évalué la performance des techniques de marquage utilisées en estimant les taux de pertes des marques et leur influence sur la croissance et la condition des poissons. Dans un deuxième temps (chapitre 2), nous avons examiné la répartition des deux espèces entre les fosses et les rapides, et nous avons quantifié les déplacements. Nous avons estimé la fidélité au site, et examiné l'influence de la taille et des densités de compétiteurs sur les déplacements. Nous avons également vérifié si les mouvements entre les habitats étaient directionnels. Enfin, dans un troisième temps (chapitre 3), nous avons comparé la croissance, la condition corporelle, et la survie apparente, trois mesures de profitabilité, entre les fosses et les rapides, pour vérifier si la profitabilité

moyenne diffère entre les habitats, comme le prédisent les modèles de distribution idéale despotique et idéale par préemption.

CHAPITRE 1

Field Trials of Marking by Tattooing and Coded Wire Tagging in Stream Salmonids

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Abstract.– We conducted field trials to assess the performance of jet injections of Alcian Blue dye and full length coded wire tags (CWTs) used simultaneously to mark brook trout and juvenile Atlantic salmon ≥ 55 mm fork length. All Alcian Blue marks remained clearly visible for approximately 4 weeks (range 24-29 d). After 8 weeks (range 52-65 d), 2.2 % of 91 recaptured brook trout and 6.2 % of 64 recaptured Atlantic salmon had lost at least one mark. Dye retention was low for individuals recaptured 10 to 14 months after injection, presumably because growth of these fish caused dilution of the mark. CWT loss rates were 4.5 % (n = 67) for brook trout and 11.8 % (n = 51) for Atlantic salmon after 4 weeks, and 1.1 % (n = 92) for brook trout and 5.9 % (n = 68) for Atlantic salmon after 8 weeks. No significant differences were found between the mean length and the condition of marked and unmarked fish 4 weeks and 8 weeks after marking.

Field studies dealing with fish growth, survival, and movements frequently require marking of the fish. Which marking method is most appropriate in a given study will depend on the objectives of marking, the size and the number of fish to be marked, the duration of the study, and the influence of the marks on fish growth, survival, and behaviour. If fish are adversely affected by the mark or if, for example, mark loss rate is high or size-dependent, results may be biased. Thus, the proper use of a marking method requires knowledge about its loss rates and potential effect on the fish.

As a part of a study on the growth, habitat-specific loss rate, and movements of stream-dwelling brook trout *Salvelinus fontinalis* and juvenile Atlantic salmon *Salmo salar*, we used subcutaneous jet injection of Alcian Blue dye (tattoo marks) to batch-mark groups of fish for date and site identification, and coded wire tags (CWTs) to provide each fish with an individual mark. Alcian Blue is so far the best dye tested for tattooing fish (Cane 1981; Thedinga and Johnson 1995), with few mark losses occurring within 12 months after injection (Starkie 1975; Pitcher and Kennedy 1977; Herbinger et al. 1990; Bridcut 1993). The majority of the reports on the longevity and reliability of Alcian Blue marks, with the exception of Hart and Pitcher (1969) and Bridcut (1993), were obtained from fish held in the laboratory or under semi-natural conditions. However, Hart and Pitcher (1969) showed that Alcian Blue retention time may be shorter in the field than in the laboratory. Fading of Alcian Blue marks is directly related to the growth rate of the fish after the injection (Kelly 1967; Thedinga and Johnson 1995) and one could expect problems of dye retention with small fish growing rapidly. CWTs are small cylindrical stainless steel implants (Jefferts et al. 1963) which are commonly inserted in the snout cartilage of salmonids with high retention

(95 %; Blankenship 1990) and without altering the growth, survival, and condition of the fish (Barnes 1994). Full length CWTs (1.00 mm in length and 0.25 mm in diameter) are well-suited for marking fish > 1.8 g (approx. > 55 mm fork length; Opdycke and Zajac 1981) and recently developed half-length CWTs (0.50 x 0.25 mm) have been used successfully to mark smaller salmonids (Opdycke and Zajac 1981; Thrower and Smoker 1984). This paper reports on the retention rates of both types of mark when applied simultaneously under natural field conditions. The prerelease mortality rates associated with handling and the effect of marking on growth and condition are also discussed.

Methods

In 1993 and 1994, fish were sampled monthly from mid-June to mid-August in Chandler Creek, a tributary of the Matane River, and in two separate reaches of Gunn Creek (north Gunn and south Gunn), a tributary of the Causapscal River, in eastern Quebec, Canada (48° 25' N; 67° 07' W). At each of these study sites, fish were collected in three pool and three riffle sections. In the first sampling period (mid-June), all brook trout and Atlantic salmon captured within these sections were marked. In the second period (mid-July), newly captured fish were marked and previously captured fish were remarked. In the third and last period (mid-August), all recaptured fish plus up to 20 seemingly unmarked individuals of each species per section were conserved in a 6 % buffered formaldehyde solution for further examination.

Fish were collected with a Smith Root model 15-B backpack electroshocker (3 ms pulsed current at 700 V and 60 Hz) in sections enclosed with stop nets (5 mm mesh). Between three and six fishing passes (median = 3) were performed in an upstream direction,

waiting at least 30 minutes between consecutive passes to allow uncaptured fish to recover from electroshock (Schreck et al. 1976). Before being manipulated, captured fish were transferred to an instream tank with water circulation. Then, fish were anaesthetized individually in a tricaine solution (MS-222; 50-60 mg/l), measured to the nearest mm (fork length, FL), and weighted to the nearest 0.1 g on an electronic field balance. Fish were assigned to age groups (0, 1, and ≥ 2) according to length-frequency distributions, verified by scale reading. Fish ≥ 55 mm FL (mostly age 1 and older individuals) were tattooed with an unmodified Syrijet Mark II dental inoculator (Keystone Mizzy, Inc.) loaded with a 65 mg/ml solution of Alcian Blue (Kelly 1967; Hart and Pitcher 1969; Coombs et al. 1990; Laufle et al. 1990). The dye was injected at the base or in the rays of the pectoral (left or right), pelvic (left or right) or caudal (top or bottom) fins in different combinations to produce unique batch marks specifying the stream section and period of capture (Figure 1). The amount of dye injected was adjusted according to the size of the fish. For the smallest fish (< 75 mm FL), dye had to be injected in the fin rays whereas larger ones could be marked at the base as well in the rays of the fin. Each fish ≥ 55 mm FL also received a full length CWT (Northwest Marine Technology) with a unique binary code. CWTs codes were read under a stereoscopic microscope in the laboratory before field use (at least two readings by two different persons). Tags with unclear or repeated codes were not used. At the time of first capture, the CWTs were inserted in the snout cartilage, anterior to the olfactory bulbs, using a hand-held modified syringe (Bergman et al. 1968; Figure 1). The operators attempted to insert the tag just deep enough to allow good retention while

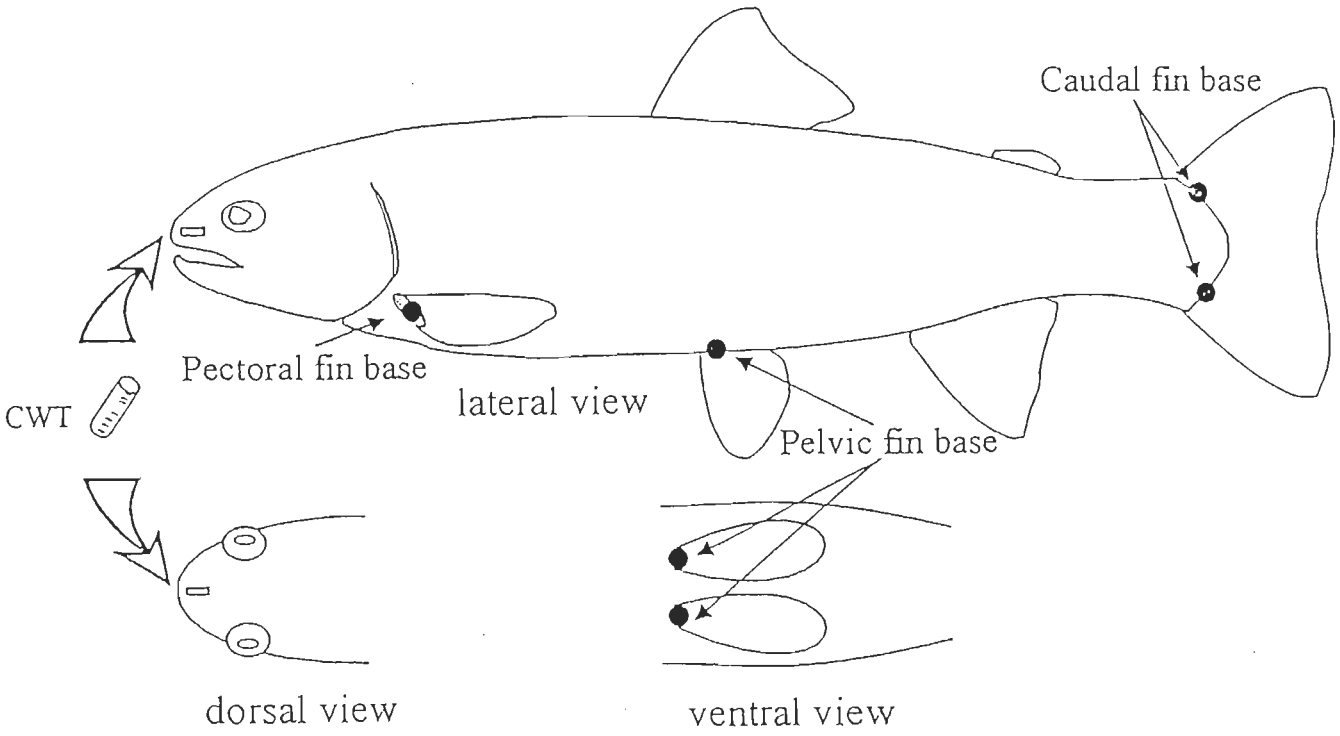

FIGURE 1. – Locations used for dye injection (black dots) and tag implantation.

avoiding damage to the olfactory nerves (Morrison et al. 1990). On the second sampling period, recaptured fish were tattooed but not tagged.

Fish < 55 mm FL (mostly age 0 individuals) were too small for marking with dye or tags and thus were batch marked by clipping the adipose fin and one of the pelvic fins for habitat-specific identification. Examination of the length of the regenerated pelvic fin allowed us to determine the marking period with precision. Individuals < 55 mm FL were excluded from the analyses in this chapter.

Fish were held in wet hands and frequently dipped into fresh, cool water during tattooing and tagging. Once marked, fish were dipped for approximately 10 s in a methylene blue solution to reduce the risk of infection. Fish passed through the entire handling process at a rate of 3-5 individuals/min. Following a recovery period of approximately one hour in an instream tank, fish were released near the center of the section. All prerelease mortalities were recorded, specifying whether death occured after electrofishing, tattooing and tagging, or tattooing alone (the latter only for individuals recaptured in the second sampling period; mid-July).

All fish kept in the last sampling period (mid-August) were examined in the laboratory to locate visible dye marks and were dissected with a magnetic scalpel to extract the CWTs. It took on average 2 min. to locate, remove, and read a tag. We assessed the retention of Alcian Blue marks for each marking location by comparing the visible marks on each fish with the mark combinations expected according to the CWT code. The number of fish that could have been misidentified due to Alcian blue mark losses was calculated by

adding the number of fish that lost at least one tattoo mark. Tag loss was measured as the percentage of recaptured fish having at least one tattoo mark but no CWT.

To assess the combined effects of electrofishing, tattooing, and tagging on growth, we performed separate analyses of variance for each species, age class, and sampling period with FL (lnX-transformed) as the dependent variable and mark, stream, and year as main factors. Analyses of covariance of body mass adjusted for FL (both lnX-transformed), stream, and year was used to examine if the condition of marked and unmarked individuals differed significantly. For these analyses, fish were assigned to two categories on the second sampling period (unmarked and marked in mid-June) and to four categories on the third sampling period (unmarked, marked in mid-June, marked in mid-July, and marked on both occasions).

Results

Mortality

Fish were grouped into three size classes (55 to 74 mm, 75 to 94 mm, and ≥ 95 mm) in order to examine if mortality and mark retention were size-related. Mortality rates during the prerelease period were inversely related to fish size (Table 1). Atlantic salmon were more sensitive than brook trout to electroshock; more than 50 % of Atlantic salmon mortality in each size class was related to electroshock, whereas few brook trout died during electrofishing or immediately after (Table 1). The percentages of brook trout and Atlantic salmon deaths that could be attributed to electroshock were quite similar between the two

years. However, mortality induced by marking was clearly higher the first year for both species (Table 1). This drop observed in 1994 is at least partly explained by the better holding conditions for the fish before handling procedures. In 1994, fish were held in a tank constantly supplied with flowing water directly from the stream, whereas in 1993 the tank was first filled and then fresh water was added regularly. In both years, fish ≥ 95 mm seemed very little affected by the marking process as only five brook trout (1.9 %, n = 264) and four Atlantic salmon (3.4 %, n = 118) died after tattooing or tagging in this group (Table 1).

Mark retention

All Alcian Blue marks remained clearly visible on the 64 brook trout and 45 Atlantic salmon marked in mid-July and recaptured 4 weeks (range 24-29 d) later, in mid-August (Table 2). A total of 91 brook trout and 64 Atlantic salmon were followed from mid-June to mid-August. After 8 weeks (range 52-65 d), 2 of these brook trout (2.2 %) and 4 of these Atlantic salmon (6.2 %) had lost at least one mark. Mark retention over the ca. 2-month period appeared to be somewhat lower in the caudal fin for both species (Table 2).

CWT loss rates were 4.5 % (n = 67) for brook trout and 11.8 % (n = 51) for Atlantic salmon after 4 weeks, and 1.1 % (n = 92) for brook trout and 5.9 % (n = 68) for Atlantic salmon after 8 weeks (Table 3).

In 1994, we recaptured 15 brook trout and 9 Atlantic salmon which had been marked the previous year. For these fish, the time interval between marking and recapture varied between 10 and 14 months. Interannual CWT loss rates were 20 % (n = 15) for brook trout and 0 % (n = 9) for Atlantic salmon. The long-term retention of the tattoo marks was low,

TABLE 1. - Number and percentage (in parentheses) of deaths during the prerelease period, by year, species, and size class.

Year	Size class (FL, mm)	Mortality		
		electrofishing	tattooing and CWT	tattooing alone
1993			Brook trout	
	55 ≤ FL < 75	4/99 (4.0)	25/95 (26.3)	
	75 ≤ FL < 95	2/103 (1.9)	11/101 (10.9)	
	FL ≥ 95	0/132 (0.0)	5/132 (3.8)	
			Atlantic salmon	
	55 ≤ FL < 75	18/117 (15.4)	27/99 (27.3)	
	75 ≤ FL < 95	12/98 (12.2)	11/86 (12.8)	
	FL ≥ 95	8/68 (11.8)	4/60 (6.7)	
1994			Brook trout	
	55 ≤ FL < 75	2/116 (1.7)	12/112 (10.7)	0/2 (0.0)
	75 ≤ FL < 95	2/89 (2.2)	3/75 (4.0)	1/12 (8.3)
	FL ≥ 95	3/160 (1.9)	0/132 (0.0)	0/25 (0.0)
			Atlantic salmon	
	55 ≤ FL < 75	19/135 (14.1)	6/106 (5.7)	0/10 (0.0)
	75 ≤ FL < 95	8/142 (5.6)	3/105 (2.9)	1/29 (3.4)
	FL ≥ 95	10/88 (11.4)	0/58 (0.0)	0/20 (0.0)

as 8 of the 12 brook trout (66.7 %) and 4 of the 9 Atlantic salmon (44.4 %) had lost at least one mark at the time of recapture.

Growth and condition

On the second and third sampling periods, no differences were found between the mean length of marked and unmarked brook trout and Atlantic salmon (Tables 4 and 5; Figure 2). Also, there was no significant detrimental effect of the mark on the condition of marked trout (Table 6). The condition of salmon was not influenced by the marking techniques in 1994. In mid-July 1993, unmarked salmon appeared in better condition (Post hoc Bonferroni test, $p < 0.011$; Table 7) but in mid-August, the effect was no longer apparent and, if anything, the condition of salmon marked in mid-June was significantly better than the condition of unmarked salmon (Post hoc Bonferroni test, $p = 0.001$; Table 7).

Discussion

Alcian Blue provided clear and durable marks over a ca. 2-month summer period, but mark retention was low for fish recaptured 10 to 14 months after dye application. Low retention rates over the ca. one-year period may be related to the growth of marked fish, which is one of the most important factors affecting the durability of dye marks (Kelly 1967; Herbinger et al. 1990; Thedinga and Johnson 1995). Kelly (1967) suggested that dye injection was a suitable marking technique as long as the fish did not increase in weight by more than 150 % between mark and recapture. In the present study, 10 of the 12 brook trout (83.3 %) and 4 of the 9 Atlantic salmon (44.4 %) followed interannually increased by

TABLE 2. - Number and percentage (in parentheses) of the total initial number of Alcian Blue marks still visible on recaptured individuals, by species and size class, both years combined. Also shown is the number of fish that lost at least one mark between tattooing and recapture.

Interval	Size class (FL, mm)	Marking location			Fish loosing at least one mark
		caudal fin	pectoral fin	pelvic fin	
			Brook trout		
mid-June to mid-August	55 ≤ FL < 75	9/9 (100.0)	7/7 (100.0)	6/6 (100.0)	0/15 (0.0)
	75 ≤ FL < 95	19/20 (95.0)	24/24 (100.0)	20/20 (100.0)	1/32 (3.1)
	FL ≥ 95	29/30 (96.7)	27/27 (100.0)	31/31 (100.0)	1/44 (2.3)
mid-July to mid-August	55 ≤ FL < 75	14/14 (100.0)	14/14 (100.0)	16/16 (100.0)	0/30 (0.0)
	75 ≤ FL < 95	3/3 (100.0)	5/5 (100.0)	8/8 (100.0)	0/11 (0.0)
	FL ≥ 95	12/12 (100.0)	12/12 (100.0)	14/14 (100.0)	0/23 (0.0)
			Atlantic salmon		
mid-June to mid-August	55 ≤ FL < 75	12/13 (92.3)	9/9 (100.0)	7/7 (100.0)	1/18 (5.6)
	75 ≤ FL < 95	17/19 (89.5)	9/10 (90.0)	13/13 (100.0)	2/24 (8.3)
	FL ≥ 95	18/19 (94.7)	12/12 (100.0)	7/7 (100.0)	1/22 (4.5)
mid-July to mid-August	55 ≤ FL < 75	8/8 (100.0)	5/5 (100.0)	2/2 (100.0)	0/14 (0.0)
	75 ≤ FL < 95	9/9 (100.0)	10/10 (100.0)	3/3 (100.0)	0/18 (0.0)
	FL ≥ 95	5/5 (100.0)	6/6 (100.0)	6/6 (100.0)	0/13 (0.0)

TABLE 3. - Number and percentage (in parentheses) of coded wire tag losses, by species and size class, both years combined.

Interval	Size class (FL, mm)	CWT losses	
		Brook trout	Atlantic salmon
mid-June to mid-August	55 ≤ FL < 75	1/16 (6.2)	1/19 (5.3)
	75 ≤ FL < 95	0/32 (0.0)	1/25 (4.0)
	FL ≥ 95	0/44 (0.0)	2/24 (8.3)
mid-July to mid-August	55 ≤ FL < 75	2/32 (6.2)	1/15 (6.7)
	75 ≤ FL < 95	0/11 (0.0)	3/21 (14.3)
	FL ≥ 95	1/24 (4.2)	2/15 (13.3)

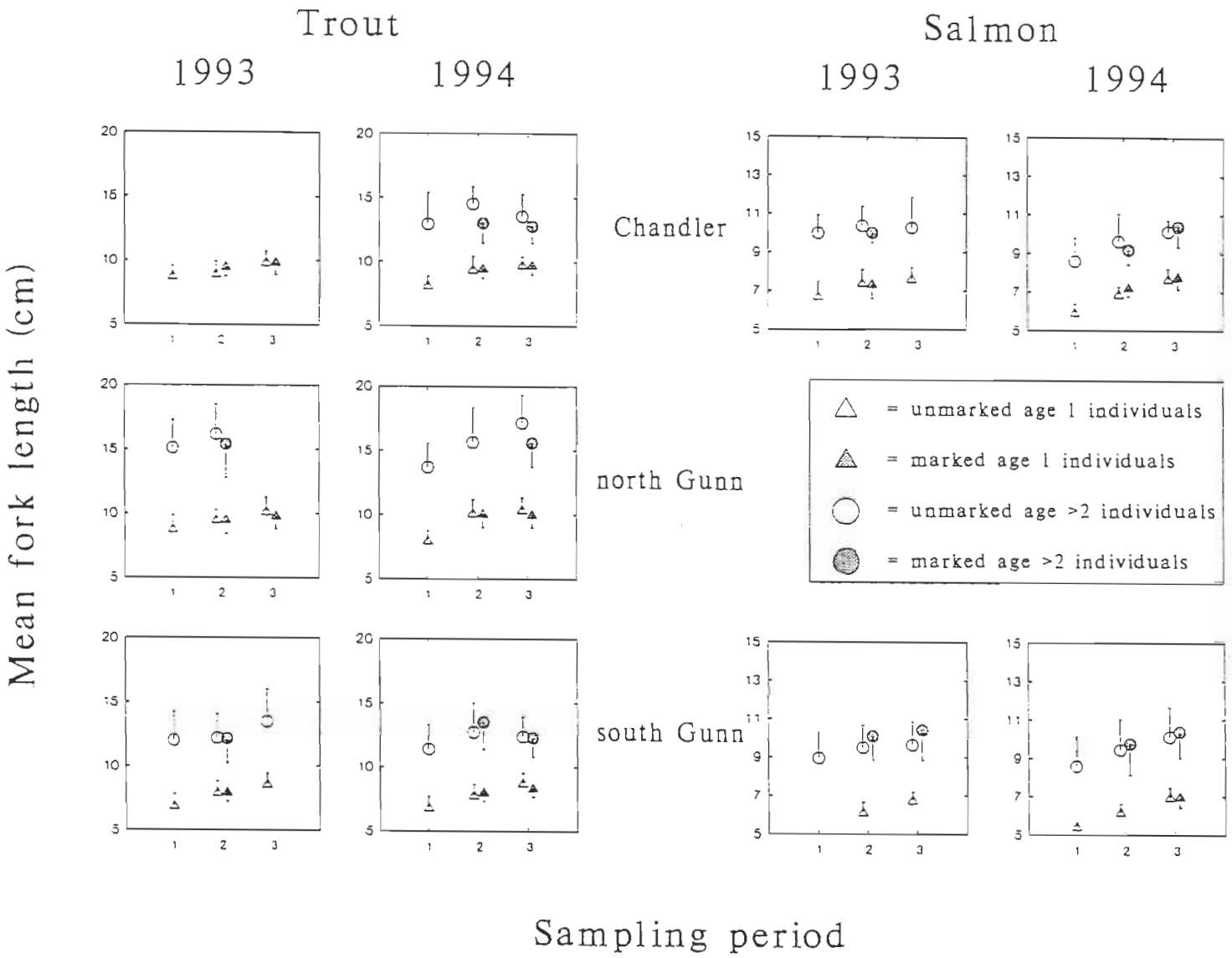

FIGURE 2. – Comparison between the mean length of marked and unmarked fish. Symbols for period 2 and 3 are shifted sligthly along the x axis to improve visibility. Error bars represent one SD. Sites in which we captured or recaptured less than 4 specimens for a given species and age class were not included in the figure. On sampling period 3, all recaptured fish were pooled in the same category (marked) as no differences in mean length were found between fish marked on the first, on the second, or on both sampling periods (Table 6).

TABLE 4. - Main effects of the ANOVA assessing the influence of the marking process on trout growth. p values for the mark effect should be assessed relative to a Bonferroni-adjusted significance value of 0.006 (0.05/8).

Year	Age	Sampling period	Effect	SS	df	MS	F	p
1993	1	2	mark	0.011	1	0.011	1.068	0.303
			stream	0.559	2	0.280	25.970	<0.001
			error	1.453	135	0.011		
		3	mark	0.015	1	0.015	1.390	0.242
			stream	0.318	2	0.159	14.273	<0.001
			error	1.014	91	0.011		
	2	2	mark	0.000	1	0.000	0.001	0.977
			stream	0.807	2	0.403	19.824	<0.001
			error	1.465	72	0.020		
		3[a]	mark	0.029	1	0.029	0.975	0.333
			stream	0.129	1	0.129	4.373	0.047
			error	0.737	25	0.029		
1994	1	2	mark	0.002	1	0.002	0.208	0.650
			stream	0.614	2	0.307	26.077	<0.001
			error	0.801	68	0.012		
		3	mark	0.046	3	0.015	1.743	0.165
			stream	0.420	2	0.210	23.970	<0.001
			error	0.718	82	0.009		
	2	2	mark	0.021	1	0.021	0.891	0.348
			stream	0.144	2	0.072	3.023	0.055
			error	1.783	75	0.024		
		3	mark	0.038	3	0.013	0.896	0.447
			stream	0.681	2	0.340	24.132	<0.001
			error	1.156	82	0.014		

[a] Analysis performed with north Gunn and south Gunn creeks data only because of insufficient cases in Chandler creek.

TABLE 5. - Main effects of the ANOVA assessing the influence of the marking process on salmon growth. p values for the mark effect should be assessed relative to a Bonferroni-adjusted significance value of 0.006 (0.05/8).

Year	Age	Sampling period	Effect	SS	df	MS	F	p
1993	1	2[a]	mark	0.001	1	0.001	0.056	0.813
			error	0.980	101	0.010		
		3[a]	mark	0.006	1	0.006	0.821	0.374
			error	0.182	25	0.007		
	2	2[b]	mark	0.003	1	0.003	0.196	0.659
			stream	0.029	1	0.029	2.175	0.143
			error	1.351	101	0.013		
		3[a]	mark	0.021	1	0.021	1.421	0.240
			stream	0.015	1	0.015	1.013	0.320
			error	0.680	45	0.015		
1994	1	2[b]	mark	0.000	1	0.000	0.018	0.893
			stream	0.078	1	0.078	17.638	<0.001
			error	0.303	69	0.004		
		3[a]	mark	0.034	3	0.011	2.158	0.105
			error	0.254	49	0.005		
	2	2[b]	mark	0.001	1	0.001	0.025	0.874
			stream	0.005	1	0.005	0.222	0.639
			error	2.328	110	0.021		
		3[b]	mark	0.014	3	0.005	0.261	0.853
			stream	0.001	1	0.001	0.064	0.801
			error	1.666	95	0.018		

[a] Analysis performed with Chandler creek data only because of insufficient cases in the other streams.

[b] Analysis performed with Chandler and south Gunn creeks data only because of insufficient cases in north Gunn creek.

TABLE 6. - Main effects of the ANCOVA assessing the influence of the marking process on trout condition. p values for the mark effect should be assessed relative to a Bonferroni-adjusted significance value of 0.013 (0.05/4).

Year	Sampling period	Effect	SS	df	MS	F	p
1993	2	mark	0.004	1	0.004	0.468	0.494
		length	125.198	1	125.198	15508.503	<0.001
		stream	0.038	2	0.019	2.325	0.100
		error	1.728	214	0.008		
	3	mark	0.002	1	0.002	0.177	0.675
		length	68.669	1	68.669	6934.742	<0.001
		stream	0.079	2	0.039	3.981	0.021
		error	1.228	124	0.010		
1994	2	mark	0.001	1	0.001	0.119	0.730
		length	100.366	1	100.366	9382.356	<0.001
		stream	0.028	2	0.014	1.307	0.274
		error	1.605	150	0.011		
	3	mark	0.003	3	0.001	0.066	0.978
		length	88.331	1	88.331	6275.141	<0.001
		stream	0.007	2	0.003	0.237	0.790
		error	2.548	181	0.014		

TABLE 7. - Main effects of the ANCOVA assessing the influence of the marking process on salmon condition. p values for the mark effect should be assessed relative to a Bonferroni-adjusted significance value of 0.013 (0.05/4).

Year	Sampling period	Effect	SS	df	MS	F	p
1993	2[a]	mark	0.050	1	0.050	6.487	0.011
		length	84.284	1	84.284	10873.201	<0.001
		stream	0.010	1	0.010	1.325	0.251
		error	1.891	244	0.008		
	3[a]	mark	0.319	1	0.319	21.931	<0.001
		length	12.037	1	12.037	827.532	<0.001
		stream	0.129	1	0.129	8.836	0.004
		error	1.775	122	0.015		
1994	2[a]	mark	0.001	1	0.001	0.213	0.645
		length	60.181	1	60.181	9568.929	<0.001
		stream	0.022	1	0.022	3.449	0.065
		error	1.145	182	0.006		
	3[a]	mark	0.017	3	0.006	0.651	0.583
		length	52.750	1	52.750	6180.335	<0.001
		stream	0.002	1	0.002	0.222	0.638
		error	1.596	187	0.009		

[a] Analysis performed with Chandler and south Gunn creeks data only because of insufficient cases in north Gunn creek.

more than 150 % in weight (brook trout: mean = 231 %, range 65 to 524 %; Atlantic salmon 130 %, 72 to 208 %) and this growth probably caused dilution of the dye. Thedinga and Johnson (1995) jet-injected juvenile coho *Oncorhynchus kisutch* and sockeye salmon *Oncorhynchus nerka* with Alcian Blue dye in the caudal fin rays and observed significant differences in mark retention between the two species after 21 weeks. They concluded that differences in growth rate probably contributed to the differences in mark longevity between species (dye retention after 10 months, coho salmon: 55 %; sockeye salmon: 73 %). Similarly, Herbinger et al. (1990) concluded that jet injection of Alcian Blue was an effective method for marking juvenile Atlantic salmon for at least 6 months, but also suggested that the rapid growth of the salmon would cause fading of the dye after a year. Alcian Blue marks consistently had longer lifetimes when applied to larger fish. Bridcut (1993) concluded that Alcian Blue marks can remain on brown trout *Salmo trutta* ≥ 85 mm FL for at least 12 months but also observed that 12.3 % of the marked trout required remarking one to two months after initial marking. As noted by Hart and Pitcher (1969), Pitcher and Kennedy (1977), and Herbinger et al. (1990), the best results on a long-term basis were obtained when dye was injected directly into the fin rays rather than in the dermal tissue only.

The ventral surface of fish smaller than 75 mm FL was easily pierced when injecting the dye. To tattoo these small fish adequately at the base or in the rays of the pectoral or pelvic fin, the strength of the jet had to be controlled precisely. If the spray was too strong, dye penetrated deeply in the body cavity and the fish was hurt. For this reason, Hart and Pitcher (1969), Herbinger et al. (1990), and Laufle et al. (1990) recommended the use of

pectoral and pelvic marks only for fish ≥ 100 mm, and caudal fin marks for smaller individuals.

CWT loss rates were 4.5 % for brook trout and 11.8 % for Atlantic salmon after 24-29 d, and 1.1 % for brook trout and 5.9 % for Atlantic salmon after 52-65 d. It appears that CWT losses were higher from mid-July to mid-August than from mid-June to mid-August. This may indicate that retention is better when the tag is inserted soon in the season or that larger fish are more likely to loose the CWT. However, the results should be regarded cautiously as these percentages are calculated on relatively small samples. We measured CWT loss rates comparable to those reported in the litterature for salmonid species. Ostergaard (1982) and Elrod and Schneider (1986) obtained CWT losses between 3 and 11 % from 1-8 d after tagging when marking hatchery-reared fingerling (96 to 118 mm in total length) lake trout *Salvelinus namaycush* before stocking. Similarly, Peterson et al. (1994) also estimated that CWT loss was 3 % approximately 7 months after marking in a wild population of juvenile coho salmon averaging 75 mm FL. Finally, Blankenship (1990) reported CWT loss rates ranging from 1.5 to 5.3 % in coho and chinook salmon weighing on average between 2.2 and 7.6 g (approx. 60-90 mm) and observed that tag loss mainly occur during the first month after tagging.

The combination of electrofishing, tattooing, and tagging appeared to have little effect on the growth and condition of fish. This is a fundamental characteristic of an ideal mark, especially if the objective of marking is to study growth, condition, or production (Wydoski and Emery 1992; Nielsen 1992). Twomey and Giller (1990) reported no significant effects of tattooing (in combination with stomach flushing) on the condition and feeding of wild brown trout ≥ 80 mm. However, repeated tattooing has been found to

depress, though not significantly, the condition of wild brown trout (Bridcut 1993). Our results agree with a number of studies that have stated that CWTs have no significant effect on the growth of wild lake trout (Elrod and Schneider 1986), captive rainbow trout *Oncorhynchus mykiss* (Barnes 1994) and chinook salmon *Oncorhynchus tshawytscha* (Eames and Hino 1983), and on the condition factor of rainbow trout (Barnes 1994).

The combination of jet injection of Alcian Blue and CWTs proved to provide batch and individual identification for at least a ca. 2 month period in summer, with few mark losses and without apparent detrimental effect on the growth and condition of the fish.

CHAPITRE 2

Movement and habitat segregation in brook trout and juvenile Atlantic salmon living sympatrically in streams

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Abstract: We examined the patterns of habitat occupancy, site fidelity, and movement of brook trout and juvenile Atlantic salmon living sympatrically in streams, and we assessed the influence of habitat type, body size, and fish densities on movement. Fish collected in nine pairs of adjacent pool and riffle sections were marked and followed over the summer in 1993 and 1994. Throughout the summer, yearling and older trout were significantly more abundant in pools than in riffles, whereas trout fry and salmon occupied the two habitats more equitably. Site fidelity was high, with recaptured individuals of age ≥ 1+ found in the pool-riffle pair of initial capture (trout = 95.4%; salmon = 91.2%; mean pair length = 24.0 m). Trout were significantly more likely to switch from riffles to pools whereas salmon switched significantly more from pools to riffles. Body size, conspecific densities, and

heterospecific densities did not significantly influence the extent of movements. The habitat occupancy and switching patterns support the notion that, in sympatry, perceived habitat profitability is higher in pools for trout and in riffles for salmon.

Résumé: Nous avons examiné l'utilisation de l'habitat, la fidélité au site et les mouvements de l'Omble de fontaine et du Saumon atlantique vivant en sympatrie dans des ruisseaux, et nous avons estimé l'influence du type d'habitat, de la taille et des densités sur les mouvements. Les poissons, récoltés dans neuf paires composées d'une section fosse adjacente à une section rapide, ont été marqués et suivis au cours de l'été en 1993 et 1994. Durant l'été, les ombles d'âge ≥ 1+ étaient significativement plus abondantes dans les fosses que dans les rapides, alors que les ombles 0+ et les saumons occupaient les deux habitats plus équitablement. La fidélité au site était élevée puisque les recaptures d'âge ≥ 1+ étaient retrouvées dans la paire fosse-rapide où ils avaient été marqués (omble = 95.4%; saumon = 91.2%; longueur moyenne des paires = 24.0 m). Le taux de mouvement des ombles était significativement plus élevé des rapides vers les fosses alors que celui du saumon était significativement plus élevé des fosses vers les rapides. La taille, les densités de conspécifiques et d'hétérospécifiques n'ont pas significativement influencé la portée des déplacements. Les patrons d'utilisation et de changement d'habitat supportent la notion selon laquelle la qualité de l'habitat perçue est plus grande dans les fosses pour l'omble, et dans les rapides pour le saumon.

Salmonids inhabiting small streams use only a subset of the wide range of habitats available to them. Physical habitat characteristics such as water velocity, depth, substratum (Symons and Heland 1978; DeGraaf and Bain 1986; Morantz et al. 1987; Heggenes and Salveit 1990; Tremblay et al. 1993), temperature and cover (Gibson and Power 1975) influence position choice in these fish. During the summer, fish may move to redistribute themselves according to habitat availability. The presence of conspecifics and heterospecifics may also modify habitat utilisation when dominant individuals exclude the subordinates from preferred positions or habitats (Fausch and White 1981; Fausch 1984). In that sense, emigration via territoriality may act as a population regulator (Elliott 1990; Grant and Kramer 1990). When two salmonid species having similar ecological demands live in sympatry, they often segregate spatially, reducing interspecies interactions (Hartman 1965; Heggenes and Saltveit 1990; Heggenes and Borgstrøm 1991). The segregation may be interactive, as a result of competition and agonistic interactions, or selective, when differences in habitat use are facilitated by genetic and morphological adaptations (Nilsson 1967). Habitat segregation often results of a combination of both factors (Hearn 1987). From the previous considerations, habitat type may be regarded as one if not the most important factor governing the spatial distribution and the movements of stream salmonids. Therefore, fish movements have to be described and quantified to fully understand population dynamics and the interactions of sympatric species. In addition, Power (1993) has pointed out that good production estimates of stream sections must take fish movements into account. In fact, fish that are lost from a section do not necessarily die and they may contribute to the production in other reaches of the stream. Milner et al. (1978) estimated

that the mobile fraction of a brown trout population contributed to approximately 30 % of the total stream production on an annual basis.

Juvenile Atlantic salmon, *Salmo salar*, frequently coexist in sympatry with brook trout, *Salvelinus fontinalis*, in small streams of eastern Canada. During the summer, trout and juvenile salmon usually defend territories or establish dominance hierarchies (Kalleberg 1958; Saunders and Gee 1964; Hunt 1965; Griffith 1972; Symons and Heland 1978; McNicol and Noakes 1981; Grant 1990) with dominant, usually larger individuals holding the most profitable positions (Fausch 1984). In allopatry, these two species are common in pool and in riffle habitats (Gibson 1973) but in sympatry, salmon displaces trout to pools (Gibson 1966; Gibson 1973; Power 1980; Gibson et al. 1993; Rodríguez 1995). Little quantitative information is available on summer movements of sympatric brook trout and juvenile Atlantic salmon. However, many studies of brown trout, *Salmo trutta*, populations alone (Jenkins 1969; Mense 1975; Solomon and Templeton 1976; Milner et al. 1979; Harcup et al. 1984; Heggenes 1988) or in sympatry with Atlantic salmon (Hesthagen 1988; Bridcut and Giller 1993), and some studies of brook trout populations in sympatry with Atlantic salmon (Keenleyside 1962; Saunders and Gee 1964; Randall and Paim 1982), concluded that stream salmonids show restricted movements before the spawning migration. Most of these studies have reported the relatively short-range movements of recaptured individuals. In a recent work on the movements of allopatric stream-dwelling brook trout, Riley et al. (1992) observed large numbers of unmarked individuals over years within their sites and suggested that many individuals were mobile.

It has been suggested that there are distinct mobile and sedentary components in salmonid populations (Funk 1955; Gerking 1959; Solomon and Templeton 1976; Harcup et al. 1984; Heggenes 1988; Hesthagen 1988; Bridcut and Giller 1993). Obviously, the costs and payoffs associated with both of these strategy (mobile vs non-mobile) are different. Territorial individuals, usually moving seldom, have a net energy intake advantage over the floater and nonterritorial schooling individuals. In fact, Puckett and Dill (1985) observed that territories owners have reduced search and prey pursuit costs compared to floater and nonterritorial schooling fish, and that they also have reduced agonistic activity costs compared to floaters. Elliott (1990) also showed that survival is positively linked to territorial possession.

Jenkins (1969) hypothesized that movement increases above a threshold level of density but the influence of fish density on movement remains unclear. Mense (1975) and Heggenes (1988) found no effect of intraspecific population density on movements of brown trout. Hesthagen (1988) found that brown trout movement rates were significantly higher at sites of high intraspecific density and also observed that trout that had moved were significantly larger than stationary individuals. The influence of fish size on movements is also unclear. Saunders and Smith (1962), Miller (1957) and Riley et al. (1992) observed that residents were larger than movers whereas Harcup et al. (1984) found no differences in length between mobile and static groups.

In this study, we evaluate habitat use and quantify the movements in sympatric populations of brook trout and juvenile Atlantic salmon followed over two consecutive summers using mark-recapture methods in two streams, eastern Quebec. We examine if

trout and salmon segregated between two habitats, pools and riffles. We assess site fidelity and examine whether the occurrence and extent of movement are related to body size, conspecific densities, and heterospecific densities. We also examine if directional habitat shifts between pools and riffles occur over the summer.

Study Area

The two study streams were located approximately 50 km south of Matane (48° 25' N; 67° 07' W), in the Matapedia Valley, Quebec, Canada (Fig. 1). Gunn Creek flows southward into the Causapscal River whereas Chandler Creek flows northward into the Matane River. There were two different sampling sites, approximately 2 km apart, on Gunn Creek (North Gunn, total length,TL ≈ 130 m and South Gunn, TL ≈ 140 m). There was another site on Chandler Creek (TL ≈ 150 m in 1993 and 375 m in 1994), located less than 10 km away from the sampling sites on Gunn Creek. North Gunn Creek is a second order tributary, whereas South Gunn and Chandler creeks are third order tributaries. At normal summer flow, stream width and maximal depth did not exceed 11 m and 1 m, respectively.

Three pairs of adjacent pool and riffle sections were chosen at each of the three sites. On average across the summers of 1993 and 1994, riffles had a mean area, a mean water velocity, and a mean maximal depth of 81 m^2, 39 cm/s, and 35 cm, respectively. For pools, these values were 56 m^2, 16 cm/s, and 72 cm. All pool-riffle pairs were separated by stream portions that were not sampled (Fig. 2). The same stream sections, identified with permanent marks on the streams bank, were sampled during the two summers with the exception of the

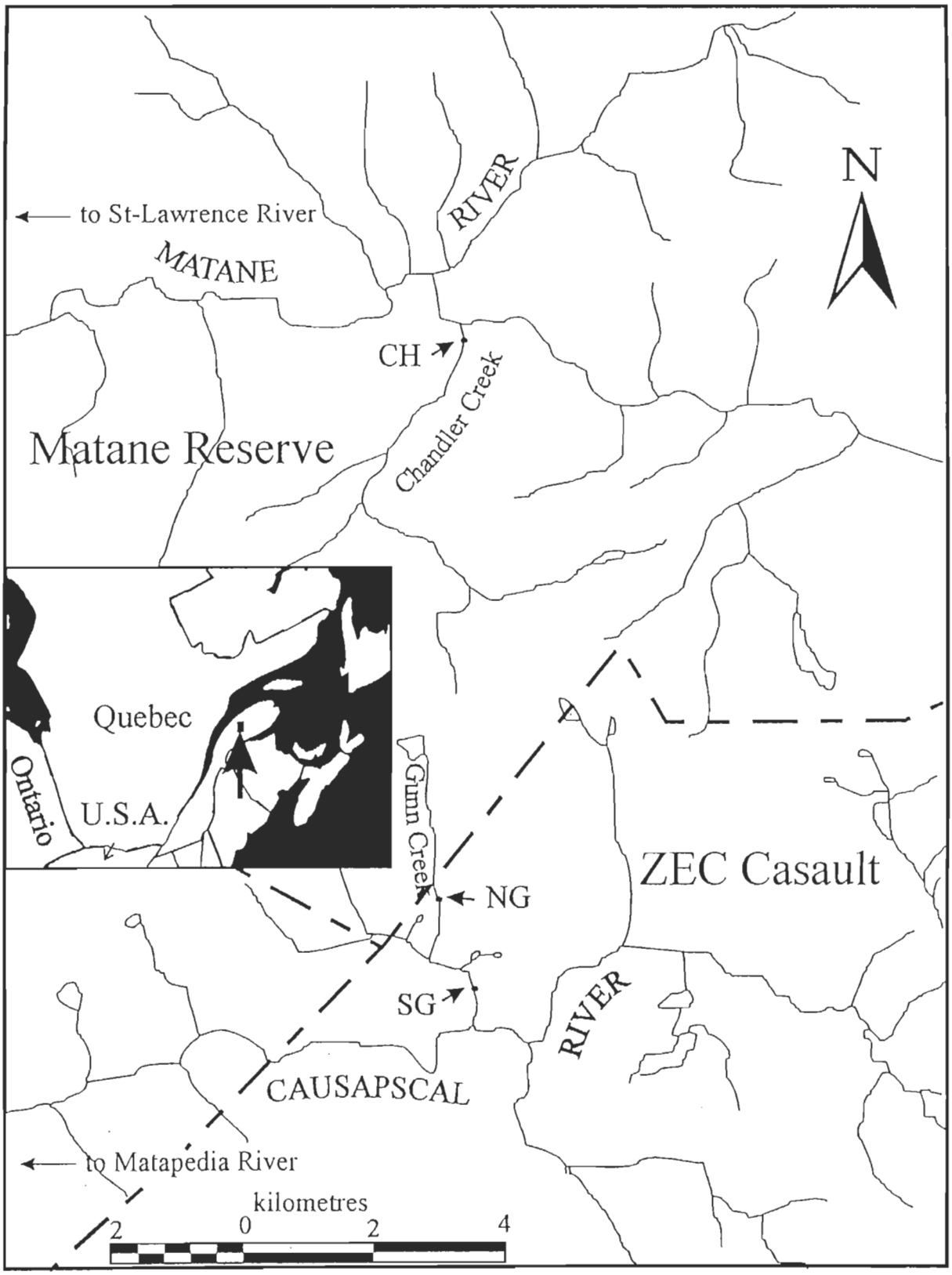

FIG. 1. Location of the study sites on Chandler Creek (CH) and Gunn Creek (North Gunn, NG and South Gunn, SG).

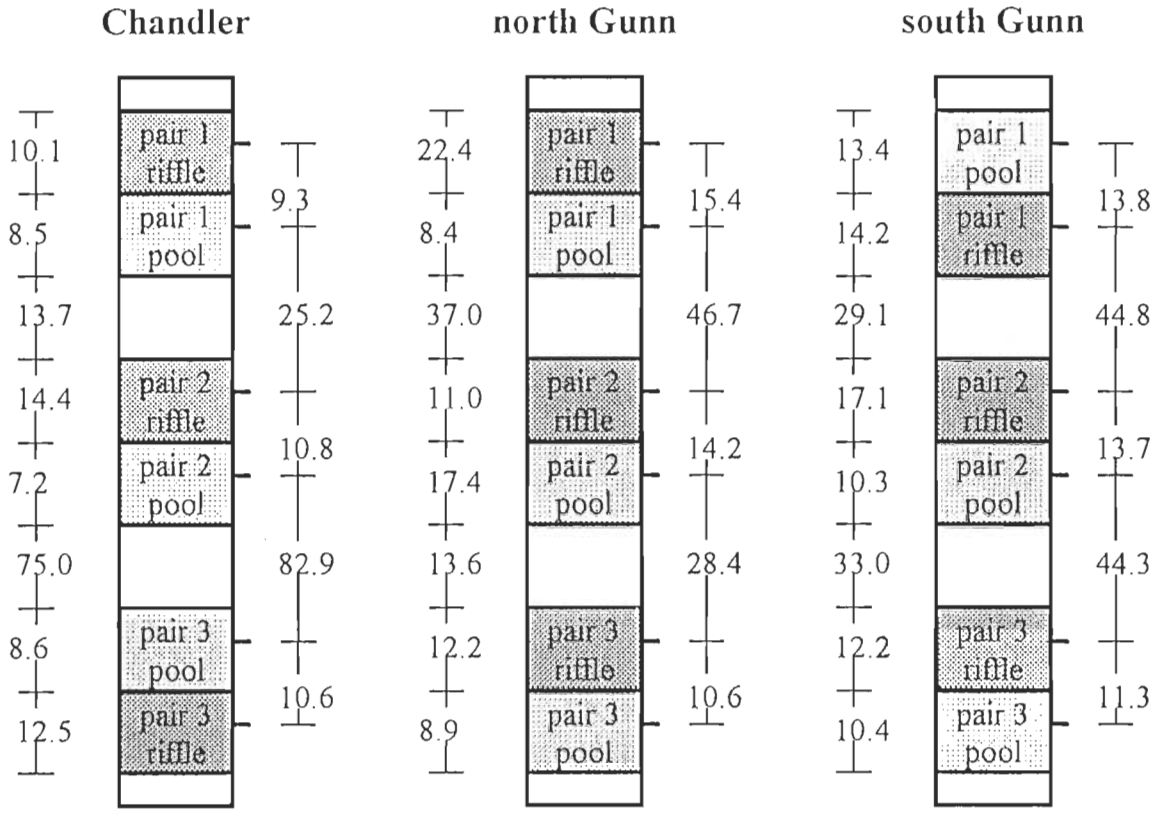

FIG. 2. Schematic representation of sampling sites (not to scale). The length (m) of each section (on the left side) and the distance (m) between the center of adjacent sections (on the right side) are shown. Blank spaces between pool-riffle pairs were not sampled. Downstream sections are at the top of the figure.

third pair on Chandler Creek which was relocated approximately 225 m upstream from its original location the second summer. The third section had to be relocated in 1994 because of important habitat alterations caused by human activities.

Brook trout and Atlantic salmon were the only fish species found in Gunn Creek. In Chandler Creek, slimy sculpin (*Cottus cognatus*) (mean density ± SE; 15.5 ± 2.0 ind./100 m^2), longnose dace (*Rhinichthys cataractae*) (2.9 ± 0.5 ind./100 m^2), and northern creek chub (*Semotilus atromaculatus*) (0.9 ± 0.5 ind./100 m^2), were present also.

Methods

The nine pool-riffle pairs were sampled by three times during the summer in 1993 (14-25 June, 13-23 July, and 9-20 August) and 1994 (9-27 June, 16-24 July, and 13-20 August; Fig. 3). In the first sampling period (mid-June), all captured fish were marked. In the second period (mid-July), fish were marked or remarked, and in the third period (mid-August), all recaptured fish were kept and conserved in a 6 % buffered formaldehyde solution. Both sections in each pool-riffle pair were sampled the same day between 6:30 and 20:00 with a Smith Root model 15-B backpack electroshocker. Fishing was conducted exclusively during day time because brook trout and juvenile Atlantic salmon, which are diurnal fish, usually feed and are more exposed to predators under daylight. On the other hand, at night, both species are often seen resting on the bottom in quiet water (Gibson 1966). Thus, we sampled these fish during their activity period, when the observations are more likely to have biological significance. Detailed information about the sampling and marking techniques used, and their efficacy, are described in Chapter 1.

Data from consecutive electrofishing passes were used in conjunction with the generalized removal model in program CAPTURE (Rexstad and Burnham 1991) to estimate the numerical abundance for each species and age group separately. Local densities were estimated by dividing numerical abundance by section area. Densities were measured in m^2 which is the unit commonly used to quantify the productivity in a stream. For both species, we calculated the percent occupancy of pools for each pool-riffle pair as follows:

$$\% \text{ occupancy of pool} = \frac{\text{density in pool}}{(\text{density in pool} + \text{density in riffle})} \; 100$$

Pairs in which we captured less than 5 specimens for a given species and age class were omitted when calculating percent occupancy of pools. To assess the effect of age and year on habitat occupancy, we applied an arcsine-square-root transformation to the percentages and used a repeated measures factorial analysis of variance with age and year as main effects and sampling period as the trial factor. Because the sections were sampled on three occasions each year, we used the multivariate Hotelling's T^2 test to verify if percent occupancy of pools differed significantly from 50 % for each species and age class when taking into account the autocorrelation of the samples.

The extent of fish movement was measured as the distance between the center of the section of recapture and the center of the section of previous capture (Heggenes 1988; Hesthagen 1988). The recapture frequency was adjusted for area by dividing the number of recaptures by section area (Hume and Parkinson 1987). For those individuals captured in all

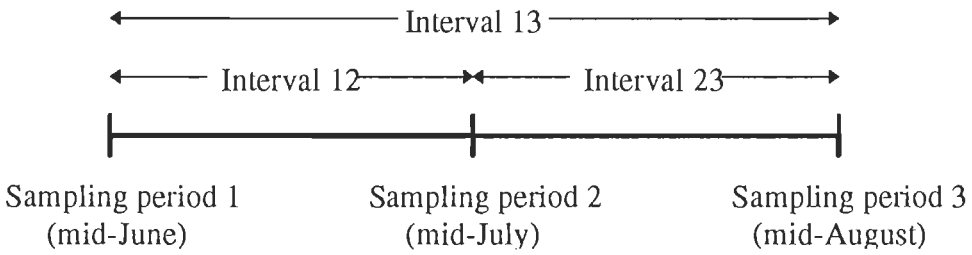

FIG. 3. Sampling schedule for 1993 and 1994.

three sampling periods, we used movements between sampling periods 1-2 (interval I12) and 2-3 (I23) for data analysis (Fig. 3).

To assess directionality in habitat shifts, we classified all recaptured fish by species, age, sampling interval, year, initial habitat type, and habitat switch (yes or no). In this analysis, we included all recaptured fish: those marked by fin clipping as well as those marked with alcian blue dye. For recaptures marked by fins clipping, we hypothesized that they remained within the same pair of sections between samplings for two reasons: more than 90 % of recaptured individuals marked with alcian blue stayed in the same pair of sections and preliminary results revealed no differences in movement behavior among age groups. We used stepwise logistic regression to examine whether the decision to switch habitats depended on the initial habitat after statistically accounting for the effects of age, conspecific and heterospecific densities, interval, year, and section areas. As the number of fish moving between the sections within a pair could be biased by the unequal areas of the 2 sections, we created a covariable (ACOV) adjusting for the area effect. ACOV was calculated as ln (riffle area/pool area) for pools and as ln (pool area/riffle area) for riffles. To properly adjust for the area effect, individuals that moved out of their pool-riffle pair of origin (trout = 4.6 %; salmon = 8.8 %) were not included in the analysis. The logistic regression allowed us to estimate the odds ratio between the probability of switching habitat type and the probability of staying.

$$\text{odds ratio} = \frac{P\text{switch}}{P\text{stay}} = e^{c}\ e^{n_1 x_1}\ e^{n_2 x_2}\ e^{n_3 x_3} \ldots\ e^{n_n x_n}$$

where Pswitch = 1 - Pstay, c = a constant, $a_1,...,a_n$ = regression coefficients, $x_1,...,x_n$ = independent variables (e.g. initial habitat, age, year, sampling interval, fish densities, section area), and n is the number of independent variables. The statistical analyses were performed with program SYSTAT 6.0 (Engelman and Wilkinson 1994; Wilkinson and Coward 1994).

Results

Habitat occupancy

Yearling and older trout were significantly more abundant in pools than in riffles (Hotelling's T^2, 1+: $p < 0.001$; 2+: $p < 0.001$). Although, there was a tendency for trout fry to be more abundant in pools than in riffles, the differences in mean density between the two habitats were not significant ($p = 0.250$) (Fig. 4). Salmon used the two habitats more equitably than trout (Fig. 4). Yearling salmon densities were slightly higher in riffles than in pools but not significantly so ($p = 0.175$). Densities of age 2+ and older salmon were more evenly distributed between habitats ($p = 0.626$) (Fig. 4). Regardless of year, sampling period and age group, total trout density averaged 63.0 individuals/100 m^2 in the nine pool sections (range across the sections: 5.3-198.6 ind./100 m^2) and 34.7 ind./100 m^2 in the nine riffle sections (range: 0-130.9 ind./100 m^2). For the salmon, a mean density of 15.1 ind./100 m^2 (range: 0-86.5 ind./100 m^2) was measured in pools compared to 17.4 ind./100 m^2 (range: 0-53.4 ind./100 m^2) in riffles. Salmon fry were scarce in our samples. The age effect is

significant for trout (repeated mesures ANOVA, $p < 0.001$), indicating differences in habitat use among age classes as pool utilisation increased with age (Fig. 4). The age effect is not significant for the salmon ($p = 0.136$). Age 2+ salmon selected pool habitats to a greater extent than yearling individuals but differences were not significant (Fig. 4). Patterns of habitat occupancy do not differ among sampling periods (trout: $p = 0.577$; salmon: $p = 0.378$) and years (trout: $p = 0.499$; salmon: $p = 0.909$) as the proportion of individuals in each habitat remained unchanged throughout the summer and between years, for both trout and salmon (Fig. 4).

Site Fidelity and Local Movements

Recaptured individuals mostly showed limited movements between sampling periods: 278 (79.2 %) of the 351 trout and 235 (79.1 %) of the 297 salmon recaptured were found within the same pool or riffle section where they had been previously marked (Fig. 5). Almost all moved fish were recaptured in the adjacent section, within the same pool-riffle pair. Then, fidelity to a pair of sections was very high: 95.4 % ($n = 335$) for the trout and 91.6 % ($n = 272$) for the salmon. Movements greater than 30 m were not frequent (trout: 4.3 %, $n = 15$; salmon: 7.4 %, $n = 22$). Only 3 salmon and 1 trout moved to a section more than 100 m away from the section where previously captured. The greatest distance recorded within our study sites, 345 m, was covered in a downstream direction by a salmon between mid-July and mid-August in 1994.

In 1994, 16 trout and 12 salmon which were marked in 1993 were caught and kept for tags reading. Approximately 12 months later, respectively 13 and 8 of these trout and

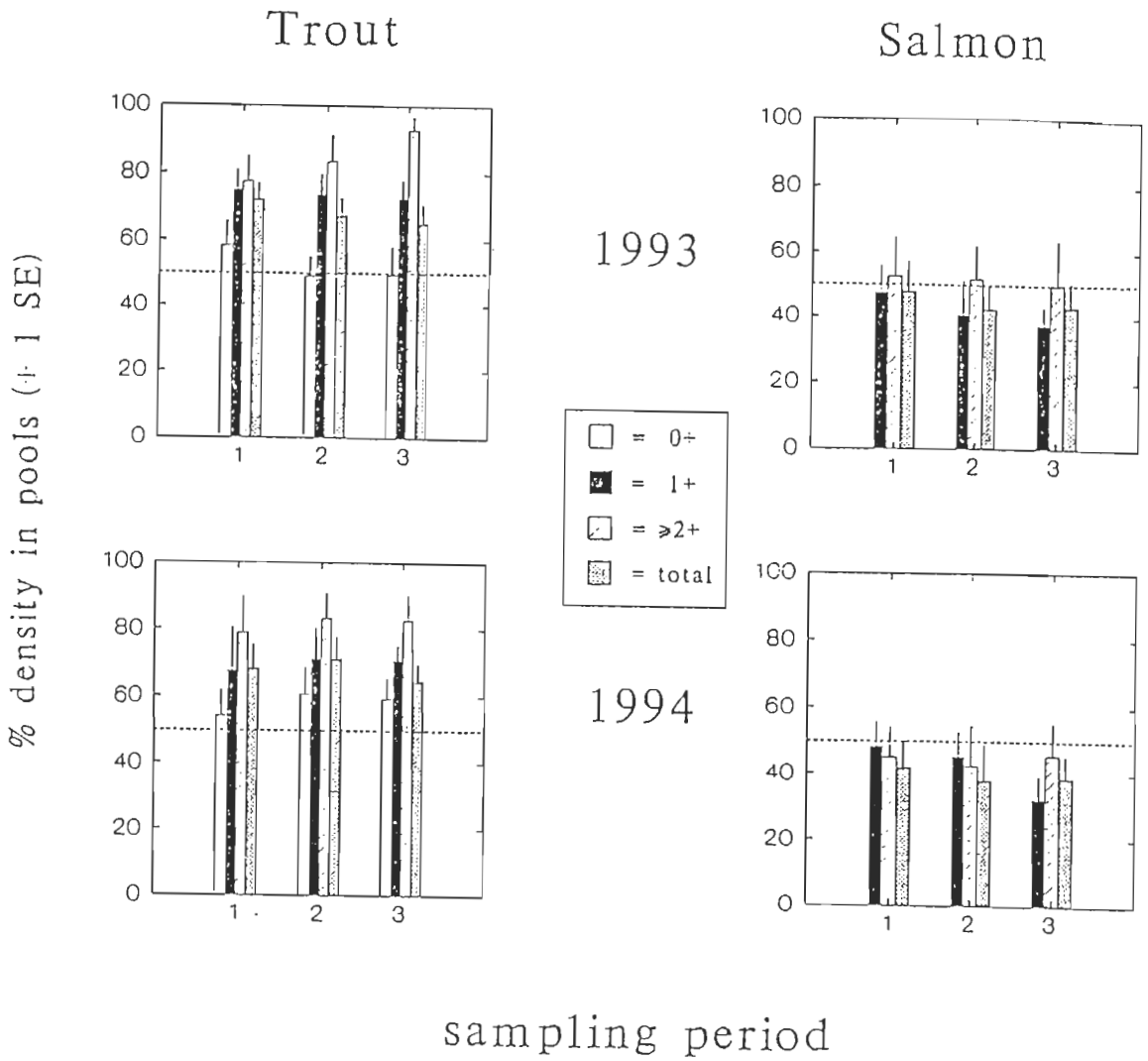

FIG. 4. Average percentage of trout and salmon density in pools, for each sampling period and year. The vertical lines correspond to +1 standard error. The horizontal dotted lines (50 %) indicate equal densities in pools and riffles.

salmon were recaptured exactly within the same section where they were marked initially, the 3 other trout and 2 salmon were still in the same pool-riffle pair, and 2 salmon only moved 45 m downstream.

The sigmoid curves obtained by plotting the distance moved on a probability scale indicate a non-normal distribution of movements (Fig. 6). The vertical portion of the curves represents a sedentary component in the population while the two tails are the moved fish. The symmetry observed from side to side in figures 5 and 6 suggests that fish did not move preferentially in an upstream (trout = 61.6 %, n = 45; salmon = 40.3 %, n = 25) or in a downstream (trout = 38.4 %, n = 28; salmon = 59.7 %, n = 37) direction.

Effects of Fish Size and Local Density

Fish size, trout density and salmon density had no apparent effect on the distance covered by individuals of both species (Fig. 7-8). We obtained similar results if the zero distances were excuded from the analysis.

Effect of Habitat

We used a stepwise logistic regression to identify which variables explained the summer movement between pools and riffles. We performed the analysis on two types of data. The first analysis was performed using the pooled data for each stream section. In the second analysis, each recapture was considered individually, as a single independent unit, what allowed us to include the age 0+, 1+ and $\geq$ 2+ in the model. Both methods gave similar results and, most important, the same conclusions.

For the trout, switching depended on initial habitat, sampling interval and section area (Table 1). Trout were significantly more likely to switch from riffles to pools than vice versa. Age, fish densities, and year did not influence switching for trout (Table 1). For salmon, switching was influenced only by initial habitat (Table 2): switching was significantly higher from pools to riffles than vice versa. Age, fish densities, sampling interval, and year did not significantly influenced switching in salmon (Table 2). Table 3 shows the probabilities of switching habitats as predicted by the logistic regressions using the data pooled by section.

Discussion

Age 1+ and older brook trout segregated between habitats, being significantly more abundant in the pools whereas trout fry and total salmon densities were rather similar between the two habitats. Gibson (1973) and Rodríguez (1995) suggested that salmon displaces the trout to the pools following interspecific competition, presumably by exploitative resource use and interference. Morphological adaptations such as enlarged pectoral fins and low buoyancy allow the Atlantic salmon to remain on or near the substratum, and to compete efficiently in riffles (Keenleyside 1962; Hearn 1987). On the other hand, trout have a size advantage due to their earlier emergence, and this may enable them to compete more successfully with salmon in the pools (Gibson 1981; Randall 1982; MacCrimmon et al. 1983; Rodríguez 1995). For the trout, pool utilisation increased significantly with age, in agreement with studies indicating a preference among older

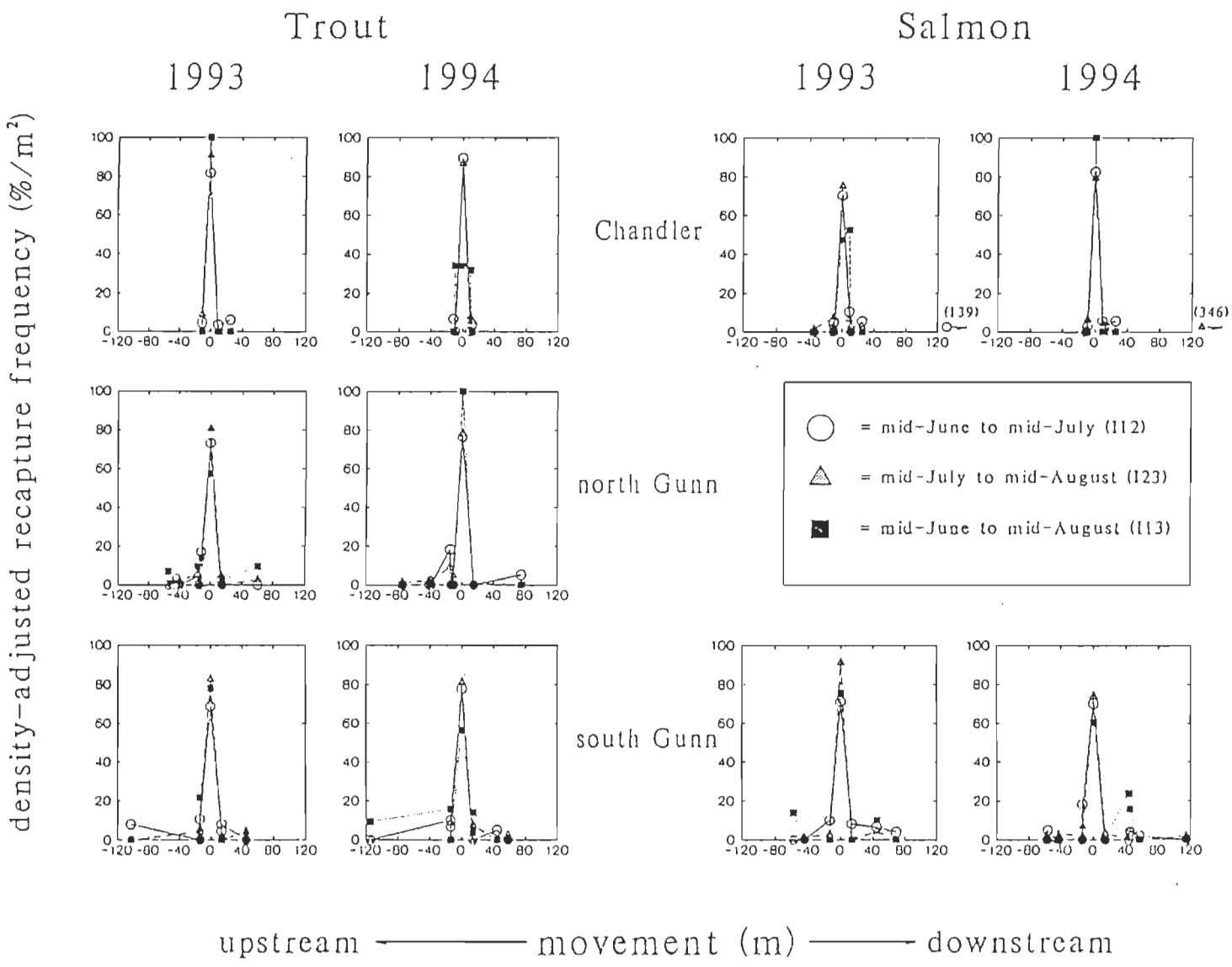

FIG. 5. Density-adjusted frequency distribution of trout and salmon movements, by year and site.

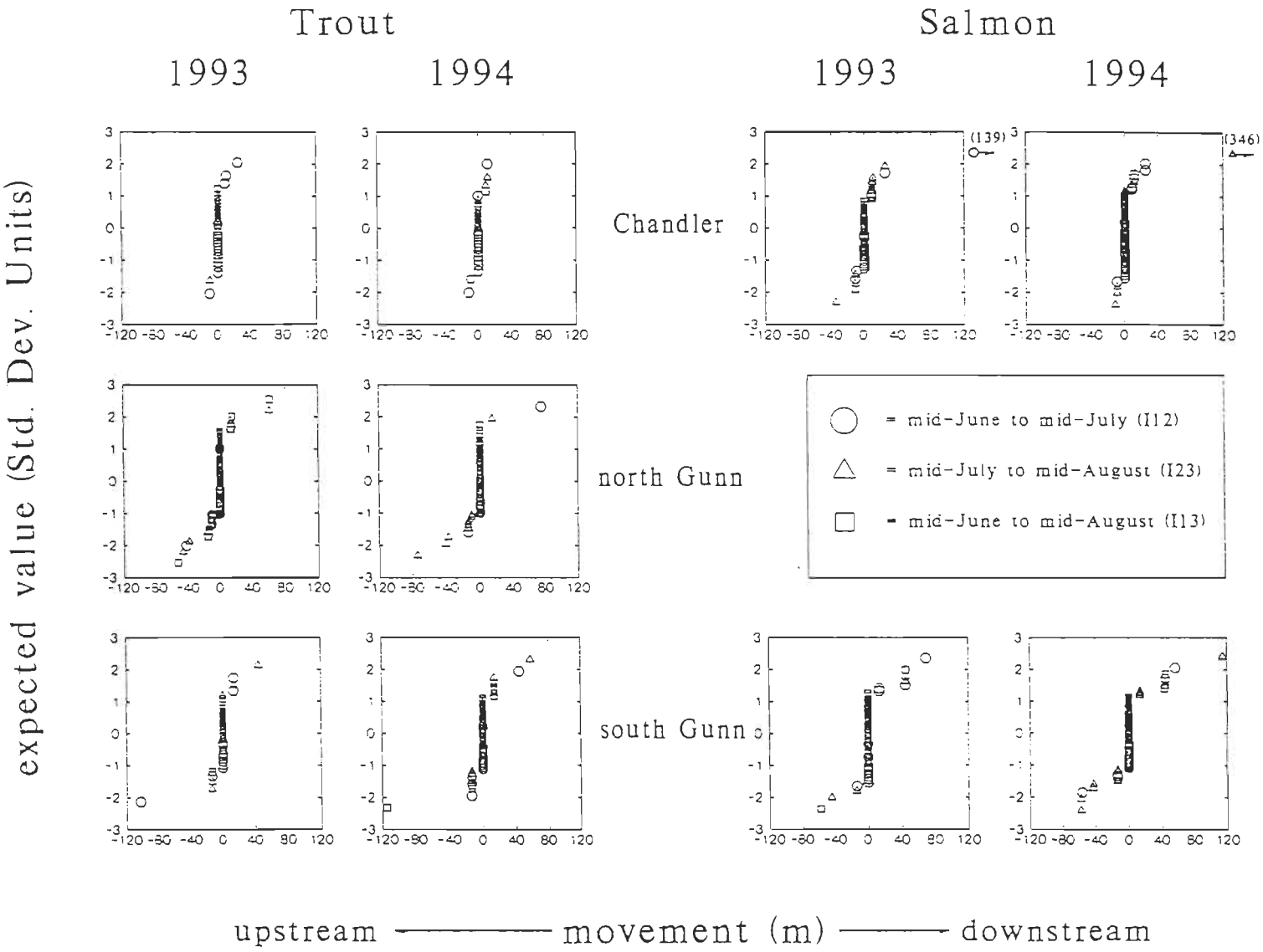

FIG. 6. Trout and salmon movement plotted on a probability scale, by year and site. A normal distribution of movements would yield a straight diagonal line with a positive slope.

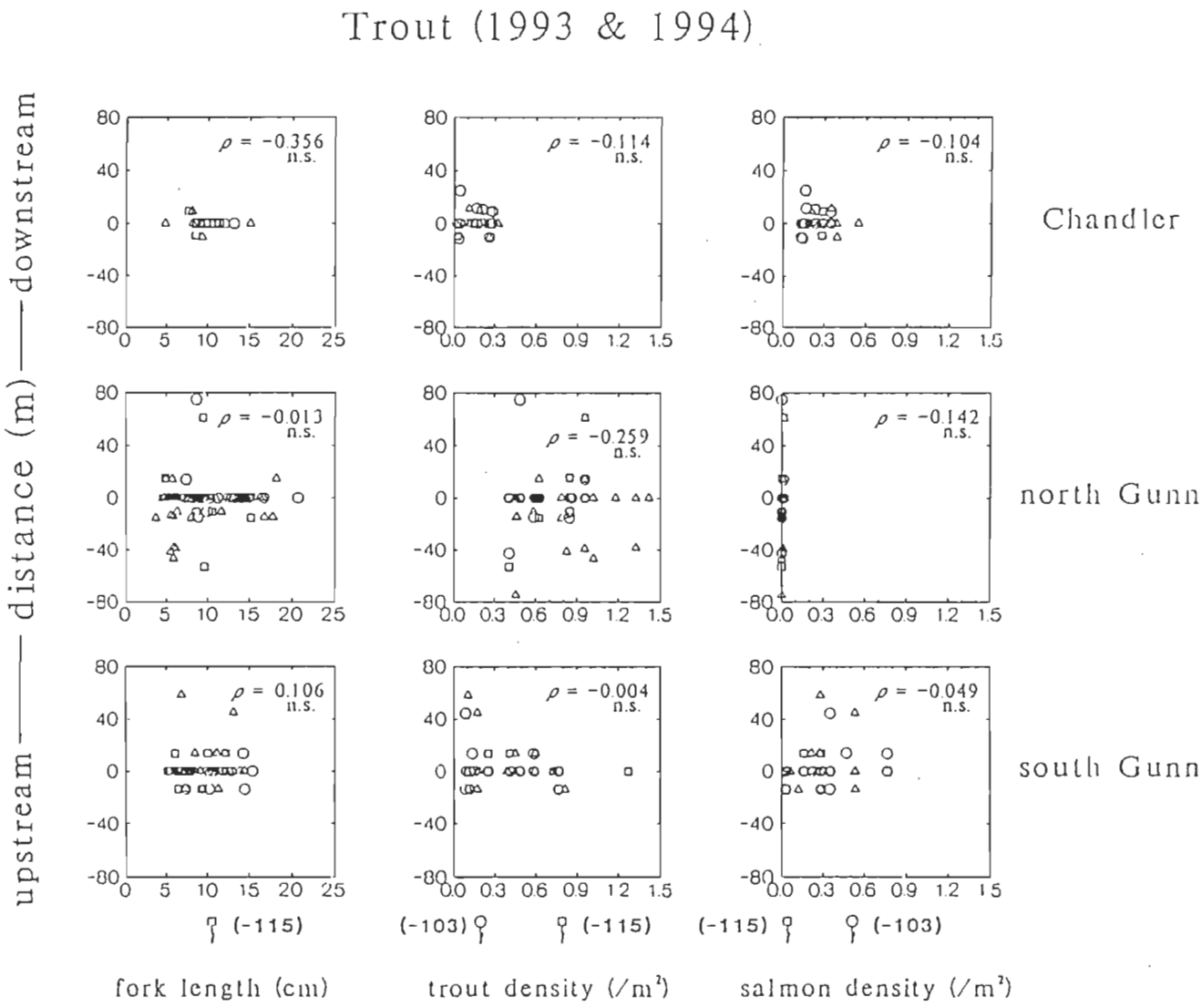

FIG. 7. Distance covered by trout in relation to the fork length of individuals before movement, trout density, and salmon density in the section before movement. ρ = Spearman correlation between | distance | and fork length or fish density; n.s. = not significant Bonferroni-adjusted probability ($p > 0.05$).

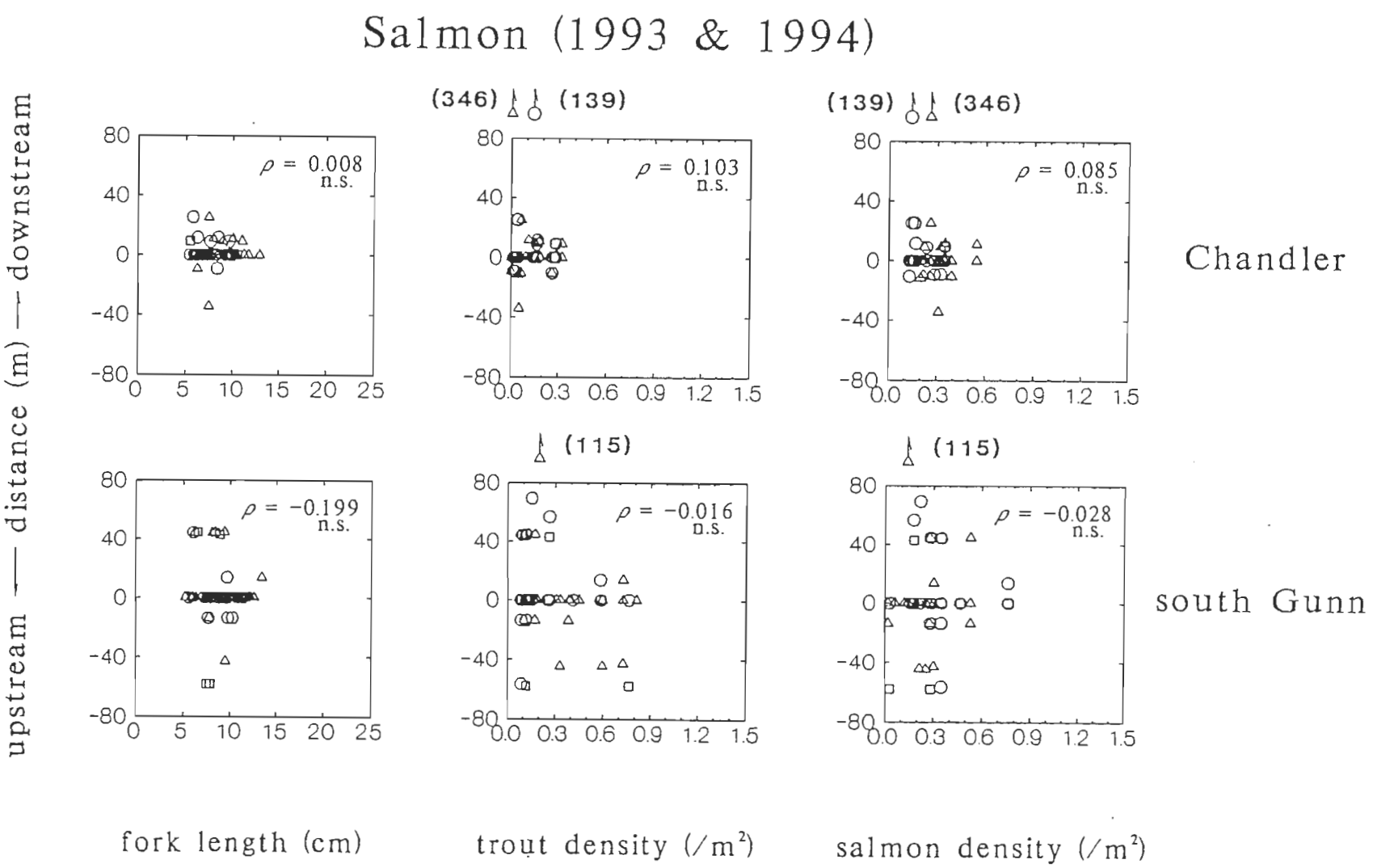

FIG. 8. Distance covered by salmon in relation to the fork length of individuals before movement, trout density, and salmon density in the section before movement. ρ = Spearman correlation between | distance | and fork length or fish density; n.s. = not significant Bonferroni-adjusted probability ($p > 0.05$).

TABLE 1. Results of the logistic regressions for habitat switching in trout.

Variables in the equation	a_i	SE	df	p	e^{ai}
With sections as sampling units (n = 91)					
CONSTANT	-0.874	0.177	1	< 0.001	0.42
INITIAL HABITAT	-0.935	0.128	1	< 0.001	0.39
INTERVAL					
I13 vs I12 & I23	0.942	0.444	1	0.037	2.57
ACOV	0.234	0.075	1	0.003	1.26
With individuals as sampling units (n = 605)					
CONSTANT	-0.643	0.172	1	< 0.001	0.53
INITIAL HABITAT	-1.124	0.246	1	< 0.001	0.32
INTERVAL			2	< 0.001	
I23 vs I12	-0.609	0.255	1	0.017	0.54
I13 vs I12 & I23	0.917	0.273	1	< 0.001	2.50
ACOV	0.748	0.169	1	< 0.001	2.11

TABLE 2. Results of the logistic regressions for habitat switching in salmon.

Variables in the equation	a_i	SE	df	p	e^{a_i}
With sections as sampling units (n = 54)					
CONSTANT	-2.176	0.092	1	< 0.001	0.11
INITIAL HABITAT	0.988	0.158	1	< 0.001	2.69
With individuals as sampling units (n = 279)					
CONSTANT	-2.430	0.279	1	< 0.001	0.09
INITIAL HABITAT	1.146	0.365	1	0.017	3.15

TABLE 3. Summer movement rates between pools and riffles as predicted by the logistic regressions.

Interval	initial habitat	stay	switch
	Trout		
mid-June to mid-July (I12) or mid-July to mid-August (I23)			
	pool	89.3	10.7
	riffle	76.6	23.4
mid-June to mid-August (I13)			
	pool	77.5	23.5
	riffle	56.1	43.9
	Salmon		
All (I12, I23, and I13)			
	pool	76.6	23.4
	riffle	89.8	10.2

individuals for deeper waters (Everest and Chapman 1972; Jones 1975; Symons and Heland 1978; Kennedy and Strange 1982; Heggenes 1988; Bridcut and Giller 1993; Gibson et al. 1993). A similar trend was observed for salmon but differences were not significant.

The densities were calculated by surface units (m^2) instead of volume units (m^3). For the salmon, which usually remains in close association with the substrate (Keenleyside 1962), this choice is obviously justified. For the trout, which often maintain its position in the water column (Keenleyside 1962), one may suspect that the technique overestimate the density in three-dimensionnal habitats such as pools, and that densities expressed by m^3 would be more appropriate in that case. However, trout density would be overestimated if trout tolerate conspecifics above or under them (i.e. if the same area, occupied by a trout at a certain depth, can be occupied at the same time by another trout at a different depth). Trout in pools adopt two types of behavior: some are territorials and chase all the intruders away from their territory. Others are nonterritorial schooling individuals which commonly hold position and forage in a structured group, with the dominant at the upstream end of the group and with the subordinates behind him (Keenleyside 1962; Gibson 1973). Therefore, given the previous considerations plus the fact that pools were relatively shallow (always less than 1m), we do think that calculating the density by m^2 was appropriate.

In the Matapedia Valley, the majority of recaptured trout (79.2 %) and salmon (79.1 %) were found in the same stream section where marked. These site fidelity rates are high despite the short length of the stream sections sampled (mean ± SE = 12.0 ± 0.6 m). Moreover, almost all recaptured fish remained within the pool-riffle pair (average pair length = 24.0 ± 1.0 m) of original capture. Spatial stability has been reported in other studies of

sympatric brook trout and Atlantic salmon (Gibson 1973; Randall and Paim 1982; Saunders and Gee 1964), brown trout (Bachman 1984; Bridcut and Giller 1993; Harcup et al. 1984; Heggenes 1988; Hesthagen 1988; Solomon and Templeton 1976), and cutthroat trout (Heggenes et al. 1991).

Funk (1955), Gerking (1959), Solomon and Templeton (1976), Flick and Webster (1975), Harcup et al. (1984), Hesthagen (1988), Heggenes et al. (1991), and Bridcut and Giller (1993) hypothesized that salmonid populations consisted of a large stationary and a small mobile component. This study of movements of brook trout and juvenile Atlantic salmon living sympatrically support their findings.

The proportions of trout and salmon moving upstream and downstream were rather similar in our study sites, agreeing with the report by Harcup et al. (1984). McFadden et al. (1967) and Shetter (1968) also measured similar proportions of trout over 18 cm moving upstream and downstream. Actually, the majority of moved fish were recaptured in the adjacent section, on average less than 15 meters away from their marking site, and few trout or salmon (trout = 4.6 %; salmon = 8.8 %) moved to another pair of sections. A tendency for brook trout to move predominantly in an upstream direction has been reported by Flick and Webster (1975) and Riley et al. (1992). Hesthagen (1988) observed a significant proportion (80.4 %) of the planted 1+ Atlantic salmon moving downstream when living sympatrically with brown trout.

At least two hypotheses may be invoked to explain the composition of the mobile component in salmonid populations. First, the mobile fraction could reflect the portion of individuals unable to defend a territory and moving most of the time. Second, most of the

fish may move occasionally so that movers always constitute a fairly constant proportion of the whole population. Even if the present study can not give support to any of these hypotheses, we believe, agreeing with most of the litterature, that the first one is more likely. Previous studies described the microhabitat selection of stream salmonids as being closely related to energy-saving reasons and concluded that a fish chooses the position that maximises its net energy intake rate (Jenkins 1969; Fausch and White 1981; Fausch 1984; Puckett and Dill 1985; Metcalfe 1986; Hughes and Dill 1990). Bachman (1984) observed that brown trout ranging in age from 0+ to 8+ stayed close to their optimal foraging site for the summer and even year after year. Individuals defending such suitable sites maximise their growth rate (Puckett and Dill 1985), their survival rate (Elliott 1990) and, ultimately, their fitness (Pyke et al. 1977). Thus, in term of optimality, maintaining a position would seem to be the best strategy. Heggenes et al. (1991) observed a few cutthroat trout moving considerable distances between every recapture when most of the individuals recaptured more than once were caught in the same stream section. However, Harcup et al. (1984) showed that brown trout individuals (> 8.5 cm in length) which had moved in one interval between sampling periods were no more likely to move in the next interval than were stationary individuals.

We found no effect of conspecific and heterospecific densities on the movement of trout and salmon as the extent of movements was not correlated with fish densities (Fig. 7-8). Mense (1975) observed in Michigan state that a 50 % reduction of the total population density of brown trout over 15 cm in total length did not affect movement patterns. Following Jenkins (1969), he suggested that population densities may affect fish movement

above a threshold level that was not reached in his study. Therefore, as suggested by Mense (1975), the effect of fish densities on movements may be hard to detect unless densities reach extreme values.

In stream-dwelling salmonids, dominant individuals usually hold positions affording maximum potential benefits (Li and Brocksen 1977; Fausch 1984; Metcalfe 1986; Rincón and Lobón-Cerviá 1993). Thus, it could be expected that dominant individuals, which are usually the larger ones (Symons 1970; Griffith 1972; Bachman 1984), remain close to their optimal stream position during the summer (Bachman 1984) while subordinates may be excluded from an area by the dominants, showing a greater rate of movements. In our study sites, body size did not help predict whether an individual would move out of a section, nor the distance it would cover. Perhaps we found no correlations between fish length and movement distance because of the limited range of fish size in our samples (Figs. 7-8). A tendency for resident salmonids to be larger than immigrants has been noted by Miller (1957) and Saunders and Smith (1962), contrary to Hesthagen (1988) who observed that mobile individuals were significantly larger than stationary ones. As the relationship between body size and fish movement is often weak or not always observed, some authors suggested that other factors such as habitat characteristics and habitat availability, are more important to explain movement behavior (Heggenes et al. 1991; Riley et al. 1992).

Riley et al. (1992) suggested that habitat may be the ultimate factor governing movements in small streams, where habitats are often distributed in a patchy mosaic. Throughout the summer, trout shifted preferentially from riffles to pools, whereas salmon shifted preferentially from pools to riffles. Directional movement from riffles to pools has

been reported for the brown trout in an Ireland stream (Bridcut and Giller 1993). There, within the study sites, trout marked initially in riffle habitats moved significantly more towards pools (mean ± SE = 51.2 ± 14.0 %) than trout marked initially in pools moved towards riffles (13.1 ± 5.0 %). However, these authors did not adjust the observed movement rates in term of the unequal area occupied by the two habitat types within the 5 study sites, and riffle habitats dominated in 4 of these. Similarly, stationary cutthroat trout from a small coastal stream in British Columbia were found to use deeper stream areas compared to mobile fish (Heggenes et al. 1991). Habitat type has also been reported to influence the dispersal pattern of stocked fish in a Virginia mountain stream. In fact, hatchery-reared brook, brown and rainbow trout individuals stocked in May into pools moved less than those stocked into riffles (25 % compared to 61 % on average for the three species) (Helfrich and Kendall 1982).

The proportion of individuals of both species in each habitat remained unchanged throughout the summer despite the directionality in habitat switching, presumably because trout were more abundant in pools and salmon were slightly more abundant in riffles. In fact, we detected significant differences between the percentages of trout and salmon moving from one habitat to the other. However, the actual number of trout and salmon moving in each direction were rather similar when taking into account the relative abundance of both species in each habitat.

The habitat occupancy and switching patterns support the notion that in sympatry, perceived habitat profitability is higher in pools for the trout and in riffles for the salmon.

CHAPITRE 3

Habitat-specific growth, condition, and apparent survival in sympatric brook trout and juvenile Atlantic salmon

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Abstract: We compared the densities, growth, condition, and apparent survival (1 - loss rate) of sympatric brook trout and juvenile Atlantic salmon in pool and riffle habitats, to examine if profitability differed between the two habitats for each species. Fish sampled by electrofishing in 9 pools and 9 riffles were marked individually and followed over the summer in 1993 and 1994. Trout densities were significantly higher in pools than in riffles, whereas salmon densities were comparable in the two habitats. For the two species, growth rates and condition were similar in pools and riffles. The apparent survival of salmon was significantly higher in riffles than in pools. The opposite trend was observed fro the trout but

the estimates were more variable than for salmon and the differences were not statistically significant. These findings suggest that salmon are « non-free » in their distribution, which is probably the result of dominance or site pre-emption. On the other hand, we could not reject the hypothesis that trout distribution was ideal free, i.e., that their density was adjusted in relation to habitat quality so that each individual has the same rewards.

Résumé: Nous avons comparé la densité, la croissance, la condition corporelle, et la survie apparente de l'Omble de fontaine et du Saumon atlantique juvénile en sympatrie, afin d'examiner si la profitabilité diffère entre les habitats pour chacune des espèces. Les poissons, récoltés par pêche électrique dans 9 fosses et 9 rapides, furent marqués individuellement et suivis durant l'été en 1993 et 1994. La densité d'ombles était significativement plus élevée dans les fosses que dans les rapides alors que la densité de saumon était comparable dans les deux habitats. Pour les deux espèces, la croissance et la condition étaient semblables dans les fosses et les rapides. Pour l'omble, la survie apparente était meilleure dans les fosses, mais non significativement. La survie apparente du saumon était significativement meilleure dans les rapides que dans les fosses. La tendance inverse a été observée pour l'omble mais les estimés étaient beacoup plus variables que ceux du saumon et les différences n'étaient pas significatives. Les résultats suggèrent que la distribution du saumon est « non-libre » et probablement influencée par la dominance et la préemption. Pour l'omble, nous n'avons pas pu rejeter l'hypothèse d'une distribution libre idéale, c.à.d. les densités sont ajustées en fonction de la qualité de l'habitat, de façon à ce que tous les individus profitent des ressources de façon équitable.

Density-dependent habitat selection models assume that the optimal habitat choice of an individual in an heterogeneous environment will be influenced by the decisions of other individuals competing for the same limited resources (space, food, shelter). Two basic assumptions of these models are that habitat profitability declines with increasing conspecific and heterospecific densities and that an individual will select the habitat in which its fitness is greatest. In the ideal free distribution model (Fretwell and Lucas 1970), there is no aggressive behavior and individuals are free to move between habitats. The richer habitat is colonized the point where resource depletion renders it comparable to the poorer habitat. The model predicts that the average fitness across all occupied habitats will be equal when habitats are filled. In contrast, in the ideal despotic (Fretwell and Lucas 1970) and ideal pre-emptive models (Pulliam and Danielson 1991), newcomers may be deprived from resources by dominant individuals or previous occupants and be forced into lower quality areas. In these models, the fitness of the lowest ranking individuals is equalized among habitats but the average fitness should be lower in the poorer habitat. These predictions of habitat selection models have been tested successfully in monospecific contexts with small rodents (Morris 1989; Halama and Dueser 1994), cervids (Wahlström and Kjellander 1995), birds (Krebs 1971), and insects (Whitham 1978) by comparing fitness measures between habitats.

In northeastern America, brook trout, *Salvelinus fontinalis*, and juvenile Atlantic salmon, *Salmo salar*, frequently coexist in the same streams and segregate spatially, trout being more abundant in pools and salmon being more abundant in riffles (Saunders and Gee 1964; Gibson 1973; Power 1980). Both species feed mainly on drifting invertebrates

(Keenleyside 1962; Gibson et al. 1984; Thonney and Gibson 1989). The drifting invertebrate delivery rate (Gibson 1981) and the density of benthic invertebrates (Schlosser and Ebel 1989) differ between pools and riffles mainly because of differences in water velocity and productivity between the two habitats. From the last consideration, one might expect that both species prefer riffle habitat. However, differences between pools and riffles with regard to water velocity, depth, and substratum may modify the foraging efficacy and the relative competitive ability of each species between habitats. For example, fish in riffles may potentially benefit from more feeding occasions (Everest and Chapman 1972; Wankowski and Thorpe 1979; Fausch 1984), but must also face higher energy expenditure associated with position maintenance, feeding forays, and agonistic activities (Fausch and White 1981; McNicol and Noakes 1984; Hughes and Dill 1990). Salmon are morphologically better adapted to riffle habitat than trout, because of their larger pectoral fins and lower buoyancy. These characteristics allow salmon to exploit riffles more efficiently than trout by remaining in contact with or near the substrate. In contrast, trout are more exposed to the current and must swim actively in order to maintain position (Keenleyside 1962; Gibson 1981).

The spatial distribution of sympatric trout and salmon appears to be influenced by exploitative and interference competition (Gibson 1973, 1981). Rodríguez (1995), based on an analysis of density patterns, suggested that salmon displaces trout from riffles to pools following competition by exploitation. In pools, interspecific competition seemed to occur through exploitation and interference, the identity of the superior competitor depending on the density of each species (Rodríguez 1995).

In salmonids, growth provides an assessment of habitat profitability, as it integrates all potential energetic costs and benefits that are associated with feeding, position maintenance, movements, and social interactions over a long time scale. Fausch (1984) suggested that growth rate in salmonids is highly correlated to fitness as individuals growing rapidly should have more energy to invest in reproduction activities. Apparent survival (the complement of mortality plus emigration) and condition of fish (a measure of the state of well-being of a fish) are also useful indicators of habitat profitability in stream-dwelling salmonids (Riley and Fausch 1995). Individuals should remain resident longer in better habitats because they would probably gain little by moving elsewhere. Conversely, mobility is favored in suboptimal habitats in which individuals should reside before attempting to move into higher quality habitats (Halama and Dueser 1994; Winker et al. 1995).

In this study, we compare habitat-specific density, growth, condition, and apparent survival of sympatric brook trout and young Atlantic salmon between pools and riffles to examine if, as predicted by the ideal despotic and ideal pre-emptive models, mean fitness differs between habitats.

Study Area

This study was conducted in two streams located in the Matapedia Valley, approximately 50 km south of Matane (48° 25' N; 67° 07' W), Quebec, Canada. Two sampling sites, about two km apart, were chosen on Gunn Creek, a tributary of the Causapscal River (north Gunn, total length, TL ≈ 130 m and south Gunn, TL ≈ 140 m). There was one site on Chandler Creek, a tributary of the Matane River (TL ≈ 150 m in 1993

and 375 m in 1994), located less than 10 km away from the two other sites. North Gunn Creek is a second order tributary, whereas south Gunn and Chandler creeks are third order tributaries. At normal summer flow, stream width and maximal depth did not exceed 11 m and 1 m, respectively.

At each of these three sites, three pairs of adjacent pool and riffle sections were identified with permanent marks on the stream banks. Pools and riffles could be clearly differentiated according to physical characteristics such as water velocity and depth (Table 1). Pool-riffle pairs were separated by stream portions that were not sampled. The same stream sections were sampled during the two summers with the exception of one pair on Chandler Creek which was relocated approximately 225 m upstream in 1994. Sport fishing is forbidden within the study area.

Brook trout and Atlantic salmon were the only fish species found in Gunn Creek. In Chandler Creek, slimy sculpin (*Cottus cognatus*) (mean density ± SE; 15.5 ± 2.0 individuals/100 m^2), longnose dace (*Rhinichthys cataractae*) (2.9 ± 0.5 ind./100 m^2), and northern creek chub (*Semotilus atromaculatus*) (0.9 ± 0.5 ind./100 m^2), were present also.

Methods

Fish were collected by electrofishing in nine pool-riffle pairs (18 sections) and marked following the techniques described in Chapter 1 and the sampling schedule described in chapter 2.

Data from consecutive electrofishing passes were used in conjunction with the generalized removal estimator in program CAPTURE (Rexstad and Burnham 1991) to

Table 1: Physical characteristics of the sections sampled, by year and habitat.

Variable	Pools		Riffles	
	1993	1994	1993	1994
Mean area ± SE (m^2)	52.7 ± 3.5	59.1 ± 3.5	80.9 ± 6.0	81.1 ± 7.3
Mean water velocity ± SE (cm/s)	15.7 ± 1.7	16.6 ± 2.0	37.0 ± 2.3	41.4 ± 2.6
Mean maximal depth ± SE (cm)	71.7 ± 6.0	71.9 ± 3.2	33.1 ± 3.4	36.1 ± 1.3

estimate the numerical abundance for each species and age group separately. Local densities were calculated by dividing numerical abundance by section area. For each year, a repeated measures analysis of variance, with age and habitat as main factors and period as the trial factor, was performed on ln (X+1)-transformed densities to test for differences in trout and salmon abundance between habitats.

To estimate the mean length of recaptured individuals, we performed separate analyses of covariance on final length for each species and year, with section and period between marking and recapture as the main factors, and initial length as the covariable. Thus,

$$L_f = \text{constant} + a\,L_i + b\,S + c\,T$$

where L_f is final lenght, L_i is initial length, S is a grouping variable identifying sections, T is a grouping variable coding for the period between marking and recapture (mid-June to mid-August or mid-July to mid-August), and a, b, and c are constants. Sections in which less than 5 individuals were recaptured for a given species were omitted from the analysis. The analysis of covariance provided the mean length of recaptured individuals, adjusted for initial length and time interval, in each section, thus allowing us to estimate the growth increment for individual fish. Only fish recaptured within the same section of initial capture were used when calculating growth. We used independent t-tests for each species and year to test if growth rate differed between habitats.

On each sampling occasion, we calculated the condition factor (K) of every fish as follows:

$$K = W_{obs} / W_{pre}$$

where W_{obs} is the observed weight of the fish and W_{pre} is its predicted weight from the allometric weight-length relationship, $W = aL^b$. The constants a and b were estimated by regression analysis from the log-transformed length and weight data. A repeated measures analysis of variance with year and season as grouping vartiables was performed on the mean K value in sections with ≥ 3 individuals for a given species to determine if the condition of fish varied significantly between habitats.

We used mark-recapture data in conjunction with program SURGE (Pradel and Lebreton 1993) to calculate maximum-likelihood estimates of apparent survival (Φ) by stream section for trout and salmon of age $\geq$ 1+. We used the model considering survival and recapture probabilities constant over the summer but different between pools and riffles. To test for differences between pools and riffles, we performed a repeated measure analysis of variance for each species with Φ as the dependent variable, habitat as the main effect, and year as the trials factor. Unreliable Φ estimates, i.e. those with 95 % confidence interval from 0 to 1, were not used in the analysis. The statistical analyses were performed with the program SYSTAT 6.0 (Wilkinson and Coward 1994).

Results

Density patterns

Mean trout densities were significantly higher in pools than in riffles (repeated measures analysis of variance; 1993, $p = 0.001$; 1994, $p = 0.005$) whereas salmon densities were comparable between habitats (1993, $p = 0.902$; 1994, $p = 0.568$) (Table 2). Densities differed among ages for both trout (1993, $p = 0.005$; 1994, $p = 0.009$) and salmon (1993, $p < 0.001$; 1994, $p = 0.001$) (Table 2). The age by habitat interaction was not significant for trout (1993, $p = 0.190$; 1994, $p = 0.379$) or salmon (1993, $p = 0.820$; 1994, $p = 0.921$). The interaction between habitat and period was not significant for either species (trout: 1993, $p = 0.829$ and 1994, $p = 0.780$; salmon: 1993, $p = 0.757$ and 1994, $p = 0.262$), indicating that the density distribution between habitats remained unchanged throughout the summer in 1993 and 1994.

Growth

The analyses of covariance used to estimate the growth rates in each section yielded high multiple R^2 values for trout (1993, $R^2 = 0.97$; 1994, $R^2 = 0.99$) and salmon (1993, $R^2 = 0.96$; 1994, $R^2 = 0.94$). Thus, growth estimates were properly adjusted for initial length and it was unnecessary to partition the results by age group.

We obtained 16 reliable growth estimates for brook trout (10 in pools and 6 in riffles) and 12 for Atlantic salmon (4 in pools and 8 in riffles). In both years, the growth

Table 2: Mean trout and salmon density (individuals/100 m^2 ± SE) by year, habitat, and age.

Year	Habitat	Age			Total
		0+	1+	≥ 2+	
			Trout		
1993	Pool	26.7 ± 5.4	19.5 ± 2.3	12.0 ± 2.0	58.2 ± 7.9
	Riffle	21.2 ± 4.0	7.0 ± 1.2	1.9 ± 0.4	30.2 ± 4.9
1994	Pool	44.9 ± 9.4	11.2 ± 1.8	12.4 ± 2.0	68.5 ± 11.2
	Riffle	33.0 ± 6.9	4.0 ± 0.7	2.3 ± 0.5	39.4 ± 7.3
			Salmon		
1993	Pool	0.3 ± 0.2	8.1 ± 2.2	9.1 ± 2.9	17.5 ± 3.7
	Riffle	0.0 ± 0.0	9.8 ± 2.2	9.6 ± 2.4	19.2 ± 3.3
1994	Pool	0.4 ± 0.3	4.5 ± 1.2	7.9 ± 1.9	12.8 ± 2.6
	Riffle	0.8 ± 0.4	6.0 ± 1.2	8.4 ± 1.8	15.2 ± 2.4

rates of trout and salmon, adjusted for the summer growth period were not significantly different between pool and riffle habitats (Table 3, t-test, $p > 0.05$).

We estimated growth increments from mid-June to mid-August and from mid-July to mid-August, by incorporating the period effect in the calculations (Table 4). If fish grow at a constant rate from mid-June to mid-August, one would expect the growth increment from mid-July to mid-August to be approximately 50 % of the total growth increment from mid-June to mid-August. This appears to the case for the salmon in both years (Table 4, 1993 = 50 %; 1994 = 58 %). However, for the trout, much of the total summer growth occured before mid-July (1993 = 67 %; 1994 = 76 %; Table 4). Since temperature influences the growth of fish (Elliott et al. 1995), we compared the minimum and maximum water temperatures recorded over 4 week summer periods (data available for 1994 only). There were no significant differences in minimum or maximum stream temperatures across the 18 sections between the two intervals (Table 5; t-test, $p < 0.05$).

Condition factor

The condition of salmon was significantly higher in riffles than in pools (Table 6, $p = 0.048$), but the small difference between the two habitats (Table 6) is unlikely to have much biological significance. Trout condition did not differ between the two habitats ($p = 0.386$). The condition of trout and salmon did not change throughout the summer (trout, $p = 0.497$; salmon, $p = 0.697$) or between years (trout, $p = 0.376$; salmon, $p = 0.386$).

Table 3: Mean growth (± SE) adjusted for the length of the summer growth period, by year and habitat. Also shown are the results of the t-tests assessing the habitat effect.

Year	Adjusted mean initial size (cm) [a]	Growth increment (cm)		df	p
		pool	riffle		
		Trout			
1993	9.2	0.8 ± 0.05	0.8 ± 0.15	6	0.991
1994	9.3	0.9 ± 0.05	1.0 ± 0.08	6	0.436
		Salmon			
1993	8.8	0.7 ± 0.01	0.7 ± 0.08	5	0.603
1994	8.9	1.0 ± 0.16	0.9 ± 0.09	3	0.607

[a] The mean initial size (L_i), adjusted for section number (S) and time interval between marking and recapture (T), was calculated by isolating the term L_i in the equation: L_f = constant + aL_i + bS + cT, where L_f is the adjusted final length and a, b, and c are the regression constants.

Table 4: Mean growth increment (± SE) for the ca. 4 week and ca. 8 week summer period, by year.

year	Adjusted mean initial size (cm)	Growth increment (cm)	
		mid-July to mid-August	mid-June to mid-August
		Trout	
1993	9.2	1.2 ± 0.13	0.4 ± 0.10
1994	9.3	1.5 ± 0.06	0.4 ± 0.04
		Salmon	
1993	8.8	1.0 ± 0.10	0.5 ± 0.06
1994	8.9	1.4 ± 0.10	0.6 ± 0.08

Apparent survival

Apparent survival was estimated only for yearling and older fish. Estimates of apparent survival were significantly higher in riffles than in pools for salmon (Table 7, p = 0.029, Fig. 1). However, trout apparent survival was not higher in pools than in riffles (Table 7, p = 0.181), possibly because of the high variability of the estimates (Fig. 1). Apparent survival did not differ between years for trout (p = 0.441) but was higher in 1994 for salmon (p = 0.030).

Discussion

During the summer, trout were segregated towards pools and salmon were evenly distributed between pool and riffle habitats. This pattern of habitat occupancy remained unchanged from mid-June to mid-August in 1993 and 1994. Thus, total trout densities were, on average, 1.8 times higher in pools than in riffles.

Despite the fact that trout were significantly more abundant in pools than in riffles, the growth and the condition of individuals were comparable in the two habitats. The growth and condition of salmon were also similar among habitats. Such results would be expected if the densities of both species between habitats were adjusted according to resource availability, without resource defense by dominants, so that each individual has equal access to the limited resources, as predicted by the ideal free distribution model.

Table 5: Minimum and maximum stream temperatures (mean across the 18 sections ± SE (range) over the 4 week summer periods in 1994, and the results of the t-tests testing for differences between periods.

Température	Period		df	p
	mid-June to mid-July	mid-July to mid-August		
Minimum	9.6 ± 0.4 (6.0-14.0)	9.0 ± 0.3 (7.0-11.0)	31	0.198
Maximum	19.9 ± 0.6 (16.0-25.0)	18.8 ± 0.5 (16.5-23.0)	32	0.168

Table 6: Average condition (± SE) of trout and salmon by year and habitat type, and the significance of the main effect habitat assessed with a repeated measures ANOVA.

Year	Condition factor		df	F	p
	pool	riffle			
		Trout			
1993	1.01 ± 0.01	1.02 ± 0.01	1	0.800	0.386
1994	1.00 ± 0.01	1.02 ± 0.01			
		Salmon			
1993	0.99 ± 0.01	1.01 ± 0.01	1	5.417	0.048
1994	1.00 ± 0.01	1.01 ± 0.01			

Table 7: Mean apparent survival (± SE) of trout and salmon for a ca. 4 week period, by year and habitat type, and the significance of the habitat main effect assessed with a repeated measures ANOVA.

Year	Apparent survival		df	F	p
	pool	riffle			
		Trout			
1993	0.56 ± 0.11	0.31 ± 0.09	1	2.415	0.181
1994	0.57 ± 0.10	0.48 ± 0.20			
		Salmon			
1993	0.34 ± 0.07	0.51 ± 0.06	1	8.192	0.029
1994	0.41 ± 0.03	0.58 ± 0.05			

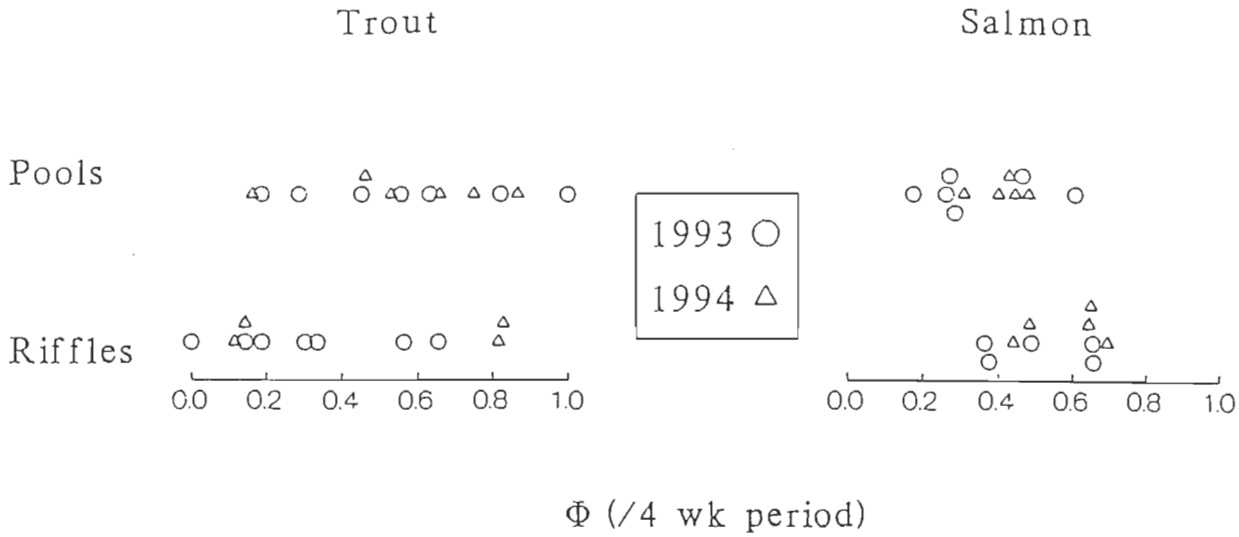

Fig. 1: Estimates of trout and salmon apparent survival (Φ) over ca. 4 week periods, by year and habitat. Symbols are shifted slightly along the Y axis to avoid overlapping.

The seasonal pattern of growth differed markedly between trout and salmon. Food abundance and water temperature are responsible for most of the variation in growth of salmonids (Elliott et al. 1995). Randall (1982) observed that brook trout fry from two tributaries of the Miramichi River, New Brunswick, reached their maximum growth slightly earlier than Atlantic salmon fry (late June versus late July) and attributed these differences to variations in stream temperature. In our streams, there is no evidence for cooler temperatures which could have enhanced trout growth rate in early summer. The decrease in trout growth rate may be related to a seasonal decrease in food consumption. In early summer, both intra- and inter-specific competition were presumably low due to high abundance of invertebrates in the drift (Gibson 1973; Gibson and Galbraith 1975) and this situation may have allowed for high growth rates in trout. As the summer progressed, competition for food may have increased following a decrease in food availability for trout as reflected by a marked seasonal decline in daily consumption rates (Guitard and Rodríguez, unpublished data). On the other hand, salmon may have been able to sustain more constant growth rates through the adoption of territoriality, which confers higher feeding rates (Grant 1990) and lower foraging costs (Puckett and Dill 1985). Symons (1971) found evidence indicating that salmon become more aggressive when food abundance is reduced.

The mark-recapture data indicated that salmon apparent survival was significantly higher in riffles than in pools. The opposite trend was observed for the trout in both years but the differences were not significant. In 1994 the magnitude of the differences between pool and riffle means for trout was as great as for salmon. However, estimates for trout

were more variable and differences were not statistically significant. The higher variability in apparent survival estimates for trout compared to salmon may be related to the greater mobility of trout. In fact, juvenile salmon are almost exclusively territorial, with individuals remaining at a fixed site most of the time when foraging or resting (Keenleyside 1962). In contrast, the territories defended by trout appear to be more temporary than those of salmon (Gibson 1973) and trout are often seen swimming freely in the water column while foraging (Keenleyside 1962; Grant and Noakes 1987). Furthermore, trout often form hierarchical groups without defending a territory (Keenleyside 1962; Gibson 1966, 1973). Thus, the trout may be less likely than salmon to remain within a section, because of differences in social behaviour and foraging techniques.

The apparent survival results suggest that profitability was highest in riffles for salmon. In fact, as emphasized by Winker et al. (1995), models of habitat use usually predict that there should be greater stability (lower turnover rates) among individuals in optimal habitats than in lower quality habitats. High-quality habitats are more likely to be colonized by dominants which would probably gain nothing by moving to another habitat. In contrast, less suitable conditions in the suboptimal habitat may favor mortality and emigration of individuals seeking better conditions elsewhere (Winker et al. 1995). Winker et al.'s (1995) hypothesis is supported by observations made by Symons (1971) and Elliott (1990) which have stated that Atlantic salmon and brown trout not acquiring a territory or in transit between territories are more susceptible to mortality than territory owners.

Between-habitat differences in apparent survival for salmon suggest that habitat use in this species is influenced by dominance or site pre-emption, in agreement with the predictions of the ideal despotic and ideal pre-emptive models of habitat selection. For the

trout, densities were significantly higher in pools, but differences in profitability among habitats were not significant. Hence, we cannot reject the hypothesis of an ideal free distribution in trout. If trout are « free » in their distribution, then their concentration in pools may equalize profitability among habitats. However, had the differences in apparent survival been statistically significant for trout, we would have concluded that trout are distributed despotically. Therefore, more precise estimates of habitat-specific apparent survival will likely improve our understanding of trout distribution.

CONCLUSIONS

Cette étude a permis la récolte de plusieurs informations importantes à la compréhension de la dynamique des populations sympatriques d'Omble de fontaine et de Saumon atlantique. Voici un sommaire des principaux résultats:

i) L'injection sous-cutanée de bleu d'alcian et l'insertion d'une CWT dans le cartilage du museau se sont avérées des techniques de marquage efficaces procurant une identification individuelle et de groupe pour une période de 8 semaines, c'est-à-dire avec peu de pertes de marques et sans effet sur la croissance et la condition des poissons.

ii) Durant l'été, l'omble est demeuré plus abondant dans les fosses que dans les rapides (différence significative pour les âges ≥ 1+ seulement). Les saumons étaient légèrement plus abondants dans les rapides, mais non significativement.

iii) Pour l'omble, l'utilisation des fosses augmentait avec l'âge, ce qui indique une préférence plus marquée des grands individus pour les eaux profondes.

iv) La fidélité au site était élevée, puisque plus de 90 % des recaptures de chaque espèce étaient retrouvés dans la même paire fosse-rapide (longueur moyenne de 24 m) où ils avaient été capturés précédemment.

v) Durant l'été, les déplacements entre les habitats étaient directionnels pour les deux espèces. Les ombles se déplaçaient proportionnellement plus des rapides vers les fosses alors que les saumons se déplaçaient plus des fosses vers les rapides.

vi) La taille et les densités de compétiteurs (conspécifiques et hétérospécifiques) n'influencaient pas les déplacements de l'omble et du saumon.

vii) La croissance de l'omble et du saumon était semblable dans les fosses et les rapides.

viii) À la fin de l'été, les deux espèces ont eu une croissance semblable. Cependant, l'omble grandit vite avant la mi-juillet et relativement peu après, alors que le saumon semble croître au même rythme du début à la fin de l'été.

ix) La condition corporelle de l'omble et du saumon ne diffère pas entre les habitats.

x) La survie apparente du saumon est significativement meilleure dans les rapides et celle de l'omble est meilleure dans les rapides, mais non-significativement.

La profitabilité est plus grande dans les rapides que dans les fosses pour le saumon. Ces résultats appuient l'hypothèse d'une distribution « non-libre » pour le saumon, c'est-à-dire une distribution où certains individus, dominants ou territoriaux, occupent les habitats les plus profitables pour l'espèce, au détriment des autres qui sont repoussés vers les moins bons sites. Pour l'omble, les densités étaient significativement plus grandes dans les fosses, mais les différences de profitabilité entre les habitats n'étaient pas significatives. Ainsi, nous ne pouvons exclure l'hypothèse d'une distribution libre idéale chez cette espèce. Si la distribution de l'omble est libre idéale, alors peut-être que la concentration des ombles dans les fosses rend le fitness moyen égal entre les habitats.

Durant l'été, la distribution spatiale de l'omble et du saumon semble être principalement affectée par des taux d'échange différentiels entre les habitats, bien que la

majorité des individus se déplacent apparemment peu. Ainsi, les taux de pertes (émigration + mortalité) pour l'omble sont plus grands dans les rapides, et le taux de déplacement sont plus élevés des rapides vers les fosses que vice versa. Inversement pour le saumon, les taux de pertes sont plus grands dans les fosses, et les déplacements sont plus importants des fosses vers les rapides que vice versa. Par contre, la croissance et la condition corporelle de chaque espèce étaient similaires dans les deux habitats.

Les aménagements modifient souvent la structure et la distribution des habitats d'un cours d'eau (p. ex.: vitesse du courant et profondeur). Il apparaît donc essentiel d'évaluer les pertes d'habitat avant d'aménager un cours d'eau abritant une population sympatrique d'ombles et de saumons. En effet, puisque la coexistence de ces deux salmonidés semblerait être étroitement liée à leur utilisation différentielle de l'habitat, un déséquilibre important dans la disponibilité de l'un ou l'autre des habitats pourrait désavantager l'une des deux espèces.

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